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Global-scale species distributions predict temperature-related changes in species composition of rocky shore communities in Britain

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Title: Global-scale species distributions predict temperature-related changes in species composition of rocky shore communities in Britain

Running title: Climate-related change in intertidal communities

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Abstract

Changes in rocky shore community composition as responses to climatic fluctuations and anthropogenic warming can be shown by changes in average species thermal affinities. In this study we derived thermal affinities for European Atlantic rocky intertidal species by matching their known distributions to patterns in average annual sea surface temperature. Average thermal affinities (the Community Temperature Index, CTI) tracked patterns in sea surface temperature from Portugal to Norway, but CTI for communities of macroalgae and plant species changed less than those composed of animal species. This reduced response was in line with the expectation that communities with a smaller range of thermal affinities among species would change less in composition along thermal gradients and over time. Local-scale patterns in CTI over wave exposure gradients suggested that canopy macroalgae allow species with ranges centred in cooler than local temperatures ("cold-affinity") to persist in otherwise too-warm conditions. In annual surveys of rocky shores, communities of animal species in Shetland showed a shift in dominance towards warm-affinity species ("thermophilization") with local warming from 1980 to 2018 but the community of plant and macroalgal species did not. From 2002 to 2018, communities in southwest Britain showed the reverse trend in CTI: declining average thermal affinities over a period of modest temperature decline. Despite the cooling, trends in species abundance were in line with the general mechanism of direction and magnitude of long-term trends depending on the difference between species thermal affinities and local temperatures. Cold-affinity species increased during cooling and warm-affinity ones decreased. The consistency of responses across different communities and with general expectations based on species thermal characteristics suggests strong predictive accuracy of responses of community composition to anthropogenic warming.

Introduction

Persistent warming is a well-established reality for the oceans, and until recently, there had been little systematic effort to synthesise the widely reported effects on biodiversity (Poloczanska *et al.*, 2013, Sorte *et al.*, 2010). Yet abundance and distributions and their changes for species living on intertidal rocky shores have long been presented as examples of responses to environmental gradients (Hutchins, 1947) and change in the oceans (Southward & Crisp, 1954b), with those in northwest Europe having been particularly well studied in relation to temperature (Crisp & Fischer-Piette, 1959, Crisp & Southward, 1958, Fischer-Piette, 1936, Southward & Crisp, 1954a, Southward & Crisp, 1954b). Increases in abundance of warm-affinity species and declines in cold-affinity ones (Mieszkowska *et al.*, 2014a, Southward, 1991, Southward *et al.*, 1995), poleward advances of species at cold range edges (e.g. Hawkins *et al.*, 2009, Herbert *et al.*, 2003,

Mieszkowska *et al.*, 2006a) and retreats of species at warm boundaries (Jones *et al.*, 2012) relative to limits in 1950s and 1960s have all been observed with warming. While species interactions such as grazing are involved in controlling abundance change across latitudinal gradients (Coleman *et al.*, 2006, Jenkins *et al.*, 2005), thermal tolerances closely follow latitudinal ranges of many species (Breeman, 1988, Sunday *et al.*, 2012), implying direct links between survival and temperature. This close link has led to simple predictions of range changes based on shifts in isotherms (Burrows *et al.*, 2011, Loarie *et al.*, 2009). Difficulties in tracking range edges over time (Bates *et al.*, 2015, Tingley & Beissinger, 2009), however, make relating range shifts to isotherm shifts impractical as a way of measuring responses to climate.

More tractably, linking changes in abundance and frequency of occurrence of species to their thermal affinity allows assessment of the effects of warming for species assemblages at defined locations. When changes have been observed over a period of warming, cold-affinity species (boreal species in northwest Europe) typically decline and warm-affinity species increase, as seen for bottom-living fishes of the European continental shelf (Genner *et al.*, 2004, Simpson *et al.*, 2011) and Mediterranean (Givan *et al.*, 2018). The prevalence of the pattern of changes in relation to thermal affinities of species suggests that "cold-affinity species decline and warm-affinity species increase with warming" may serve as a general rule, with the widely observed changes termed "thermophilization" in terrestrial vegetation (De Frenne *et al.*, 2013). Thermophilization can be measured using the weighted average of thermal affinities of species that make up a community, the Community Temperature Index (CTI). CTI change reflects changing species dominance and composition when weighted by abundance or frequency of occurrence, and turnover when weighting by presence alone. CTI has been widely used to track changes in natural communities (Devictor *et al.*, 2008), and exploited species (Cheung *et al.*, 2013), The relative contribution of each species to compositional change is attributable to their themal affinity, with increasing CTI in some places associated with declines in cold-affinity species (birds in France, Tayleur *et al.*, 2016) and increases in warm-affinity ones in others (birds in North America Princé & Zuckerberg, 2015). The difference between local temperature change and composition change expressed by CTI has been interpreted as climate 'debt' (Devictor *et al.*, 2012), the catching-up needed for community composition to track temperature changes perfectly. But smaller shifts in average thermal affinity may result from the collective responses of highly eurythermal species, or where many species share similar affinities (Burrows *et al.*, 2019, Flanagan *et al.*, 2018).

Further measures based on species thermal affinities show promise for projecting how communities might respond to climate. The difference between CTI and local temperature, termed the thermal bias, suggests local extinctions in relation to climate warming (Stuart-Smith *et al.*, 2015) where this measure is negative. Species in such places tend to have distributions centred in

colder regions than the location considered, and may face a greater threat of local extinction since they are more likely to be approaching their upper thermal limits. The range of thermal affinities, expressed as community thermal diversity (the abundance-weighted standard deviation of STIs, hereafter CTDiv), can predict the likely responsiveness of the CTI to temperature change (Bonachela *et al.*, 2019, Burrows *et al.*, 2019). Communities composed of species with similar thermal affinities are likely to change less in composition with warming or cooling than those communities composed of diverse thermal types. Similarly, communities made up of narrow-ranged species may be more responsive to temperature change with a more rapid species turnover (higher beta diversity) and faster rate of CTI change relative to temperature change. These latter effects are suggested by simulations based on species abundance-temperature curves and seen in CTI changes in bottom-trawl and plankton datasets over the last 30 years (Burrows *et al.*, 2019).

Patterns in average species thermal affinity across smaller scales can reveal thermal influences on community composition among nearby sites and the effects of thermal microclimates within sites. Communities protected from thermal extremes, such as those under forest canopies, on shaded slopes or on complex intertidal surfaces (Firth *et al.*, 2016), may be buffered from the effects of climate change. In UK grassland, CTI change is greater in exposed microclimates (Maclean *et al.*, 2015), a habitat potentially equivalent to open rock on wave-exposed shores. Wave-sheltered rocky shores in temperate regions tend to be dominated by large canopy-forming macroalgae (Burrows *et al.*, 2008, Lewis, 1964) such that temperatures under algal canopies are cooler than on nearby rock on sunny summer days (Moore *et al.*, 2007), potentially offering climatic refuges for high-temperature-sensitive species. Such complex patterns of thermal habitat variation in the rocky intertidal may mask the effects of latitudinal gradients in air and sea temperature on species distributions along continental coastlines (Helmuth *et al.*, 2006), with often greater differences among temperatures within sites than across whole-continent latitudinal gradients, and latitudinal patterns of some metrics counter to simple expectations of poleward decreases (Seabra *et al.*, 2015).

In this study, we examined evidence for temperature as a driver of community composition in spatial patterns in CTI in rocky intertidal communities using a large dataset of European surveys, and contrast responses of communities of primary producers with communities comprised of higher trophic level species. We aimed to assess the effects of wave exposure on community thermal affinity, thought to be due to local modification of thermal habitat through intertidal canopy-forming algae (Pocklington *et al.*, 2018), through associated changes in composition of higher trophic level (animal) communities. While some survey sites were not visited every year since 2002, annually repeated surveys at sites across SW Britain over two decades (17 years, 2002-2018) and over four decades (41 years, 1976-2018) for a set of sites around an oil terminal in Shetland

allowed responses of communities to changes in temperature to be measured using the CTI approach. Trends in CTI were compared with the magnitude and direction of temperature change, and were predicted to be modified positively by the diversity of thermal affinities among the constituent species (CTDiv), negatively by the average thermal range of species (CTR), and with more declines in species abundance in areas of negative thermal bias.

Materials and Methods

Thermal affinities of rocky shore species were obtained by extracting average coastal sea surface temperatures across the geographical range of each species. Each Species Temperature Index (STI) was derived as the median within-range sea temperature, with Species Thermal Range (STR), the spread of temperatures occupied (Table S1), as the difference between 10^{th} and 90^{th} percentile within-range temperatures. Species distribution ranges were derived from literature reports of species presence (Table S2). Geographical ranges were drawn as polygon shapefiles (ESRI format) encompassing coasts inside the known range of each species. Sea temperatures were taken from 1982 to 2011 averages in the NOAA Optimal Interpolated Sea Surface Temperature dataset (OISSTv2 HR, Reynolds *et al.*, 2007), using only 0.25° latitude/longitude cells adjacent to the coastline. Quantiles of within-range temperatures giving STI and STR values were area-weighted by grid cell area using the cosine of latitude. Three metrics of community thermal affinity for communities in surveys were derived from STIs and species abundance: Community Temperature Index (CTI), the abundance-weighted mean of all STIs; Community Thermal Diversity (CTDiv, Burrows et al 2019), the abundance-weighted standard deviation of all STIs; and Community Thermal Range (CTR, Burrows *et al.*, 2019), the abundance-weighted average of all STRs. The taxonomic status of all species was derived using the WORMS database (obtained using the taxize library in R, Chamberlain & Szocs, 2013). Species were further divided into animals (Kingdom Animalia) and plants/algae (Kingdoms Plantae and Chromista) for separate calculation of community thermal metrics.

Spatial patterns in Community Temperature Index on UK and European rocky shore were based on data recorded by the MarClim programme (Mieszkowska *et al.*, 2013). Trends in CTI over time used data collected on annual visits to sites in the MarClim programme since 2001 and since 1976 in the SOTEAG (Shetland Oil Terminal Environmental Advisory Group) environmental monitoring programme around Sullom Voe (Burrows *et al.*, 2002, Hiscock, 1981).

Rocky intertidal surveys for MarClim followed a common protocol, recording the abundance of conspicuous species in the parts of the habitat where they were usually found (Burrows *et al.*, 2008, Mieszkowska *et al.*, 2006b). Counts and assessments of cover in randomly placed quadrats, along with timed searches for species so infrequent that they were not likely to

appear in quadrats, were used to return the category of abundance for that species. Survey effort was controlled to complete the search for checklist species within 1-2h, and over a shoreline extent of 50-200m. The seven abundance categories ranged from "not seen" despite searching during the low-tide survey period to "superabundant". Ranks of these categories were used in subsequent analysis (0, absent; 1, Rare; 2, Occasional; 3, Frequent; 4, Common; 5, Abundant; 6, Super abundant; 7, Extremely abundant). Survey locations were recorded using handheld GPS. 2489 MarClim surveys had been completed to the end of 2018. Most locations were along the coasts of the UK and Ireland, with some on the coast of continental Europe. Survey effort was more intensive during the first phase of the MarClim project (2002-2005), with subsequent surveys extending the spatial coverage of the dataset or examining longer-term changes: 61 sites around the UK coastline have been surveyed approximately annually from 2004 to 2018 (>10 visits in 14 years). Rocky shores in Shetland were surveyed annually under the SOTEAG programme from 1976 to 2018. Fixed transects ran perpendicular to the shoreline from mean low water of spring tides to above mean high water of spring tides. Abundance (on the same categorical scales as MarClim) was estimated for each species in 3 x 0.1m horizontal strips on either side of the transect line at five shore levels, using small quadrats to aid estimation. Average species abundance category rank per transect per year across the five shore levels was used to calculate abundance-weighted CTI, CTDiv and CTR, approximately equivalent to a logarithmic or logit data transformation of abundance.

Spatial patterns in community thermal metrics were visualised by spatial averaging of values into 0.5° latitude-longitude cells, (c50 x 30km). Site-specific community thermal metrics were compared with an index of local wave exposure, the summed wave fetch (distance to the nearest point of land in 32 directional sectors (Burrows, 2012). Relationships of site-average thermal metrics with temperature and wave exposure were modelled using generalised linear models with a spherical spatial correlation structure, with goodness-of-fit expressed as equivalent R^2 determined from correlation between observed and predicted values.

Temporal trends in community thermal metrics calculated from annual site surveys were compared with local trends in sea surface temperature (SST). Change in SST was expressed as annual means for 0.25° latitude-longitude grid cells extracted from the NOAA OISST HR V2 dataset (Reynolds *et al.*, 2002). Trends in CTI were estimated using simple linear regression of values at each site in the core set of annually surveyed sites. Annual CTI changes were compared with changes in local SST using linear mixed models applied to site-specific CTI and SST, with an AR1 temporally auto-correlated error term (Pinheiro *et al.*, 2018). Sites were included in models as a random factor; either as a random intercept or random slope according to whichever model gave the lower AIC value. Trends in species abundance over time and versus sea surface temperature were evaluated using simple linear regression on annual average abundance values. Slopes of

abundance versus time and temperature in southwest Britain and Shetland were compared with species thermal affinities (STIs) to assess the expectation that warm-affinity species (STI>local temperature) would increase with warming (or decrease with cooling) and cold-affinity species would decrease with warming (and increase with cooling).

Results

Spatial patterns in community thermal metrics

The primary measure of community-level response to temperature is the average thermal affinity across species (Community Temperature Index, CTI). CTI patterns across latitudinal and regional temperature gradients can indicate how such communities may respond to changing temperatures over time. CTI values aggregated into 0.5° latitude-longitude areas (Figs 1-2) increased with sea surface temperature, but CTI for animal species (aCTI, Fig. 2a) changed more rapidly with sea surface temperature than did CTI for plants and algae (mCTI, Fig. 2b). The potential microclimatic effect of increased cover of macroalgae in wave-sheltered areas was supported by a positive relationship between wave exposure and CTI for communities composed of animal species (Table 1, Fig. 3a). No such trend in CTI was seen for communities composed of plants and algae (Fig. 3b).

High variability in thermal affinities among species (Community Thermal Diversity, CTDiv; the abundance-weighted standard deviation of species thermal midpoints) can show where change in community composition in relation to temperature is expected to be greater. CTDiv was generally higher for communities of animal species than for plants and algae (Fig. S1). CTDiv did not change with temperature for animal communities but did increase with temperature for plant-algae communities (Fig. S1, Table S4). CTDiv was higher on more wave-exposed shores than wave-sheltered shores for both animal and plant-algae communities (Fig. S1b, Table S4), increasing by 0.3°C for each order of magnitude increase in summed wave fetch.

Larger average species thermal range (Community Thermal Range, CTR) was expected to indicate reduced response of community composition to temperature, with broad-ranged species expected to change in abundance at a reduced rate with distance across their geographical ranges. CTR was similar for plant and animal communities, but declined with temperature in animal communities (Fig. S1c). CTR also declined with wave exposure (Table S4) for plant and algal species, but not animals, thus rocky intertidal communities in wave-exposed places tended to be composed of narrower-ranged species of algae than those in wave shelter (Fig. S1f).

Community Thermal Bias (CTI less local temperature) is a likely indicator of the general vulnerability of species to temperature change: negative values showing a preponderance of cold-affinity species likely to decline with warming (Stuart-Smith *et al.*, 2015) and positive values

indicating communities composed of warm-water species likely to increase in abundance with warming. Animal communities had generally positive Community Thermal Bias, being above the dashed line of equality of CTI and SST in Fig 2a. Animal species in rocky shore communities generally had global distributions that were centred in waters 1-2°C warmer than the sites surveyed. In contrast, communities of plants and algae had strongly negative thermal bias, with species having STIs that were 1-3°C colder than local temperatures (Fig. 2b).

Species richness in surveys showed considerable geographical variation alongside patterns of changing thermal composition of communities (Fig. S2). The total number of species present in a single site survey increased by 0.9 per °C increase in average annual sea surface temperature (Table 1), mostly due to an increase in animal species richness, while species richness of plants and algae declined with SST. Wave-exposed locations tended to have greater numbers of species present in surveys (+2.3 species per order of magnitude increase in summed wave fetch, Table 1), an increase in both animal species richness (+3.2 per order of magnitude, Fig S2c) and plant and algal species richness (+1.1 species per order of magnitude, Fig S2d).

Temporal trends in community thermal metrics

The two regional community time-series both showed changes in CTI over time (Fig. 4, Table 2, Tables S5 and S6 for site-specific trends). CTI declined by 0.5°C in southwest England and Wales over 17 years from 2002 to 2018, with most of the decrease in the first 10 years. CTI increased in Shetland by a similar amount, steadily rising from 1980 onwards after an initial decline post 1976. Trends in all-species CTI broadly followed the patterns of regional temperature changes in each case. In Shetland, the initial drop in CTI in the late 1970s matched a similar fall in annual SST, while the steady increase post 1980 followed the general upward SST trend. Animal-species CTI showed the same pattern as the all-species CTI in Shetland, with annual CTI values being related to annual SST anomalies (Table 2, $p<0.05$). Plant and algae-based CTI in Shetland declined significantly over the same period (Fig. 4, mCTI), and was not related to local SST. Declines in CTI for all species and separately for animals and plants and algae in southwest Britain were relatively steady over the 17-year period but were not significantly related to local SST anomalies (Table 2, site-specific CTI values versus SST anomalies: random-intercepts linear mixed model).

In southwest Britain, trends in species abundance over time (as annual averages across all sites) were strongly related to individual species thermal midpoints. During the period from 2002 to 2018, cold-affinity species of both animals and algae increased in abundance at the 60 most frequently surveyed sites (>=10 times) while warm-affinity species both increased and decreased (Fig. 5a, Fig. S3). Rate of change in species abundance over time was significantly negatively related to STI (p=0.005). When compared to annual changes in average sea surface temperature,

average annual abundance of cold water species increased with cooling (an increase in abundance divided by a decrease in SST, Fig. 5c, Fig. S3), while warm-affinity species showed a positive rate of change in abundance relative to temperature change (slope of linear regression, p=0.001). In Shetland (Fig. 5b, 5d, Fig. S4), the pattern was less consistent, with some cold-affinity species declining (*Littorina saxatilis*) during warming, while others increased (*Semibalanus balanoides*). There were fewer warm-affinity species in the community in Shetland than in southwest Britain, and many species considered as cold-affinity species in southwest Britain (*Fucus vesiculosus, Fucus spiralis*) were closer to their thermal midpoint STI in Shetland. The relationships of species trends over time and with SST change with thermal affinity were not significant (though some species exerted considerable leverage on the regression slope, notably *Semibalanus balanoides*).

Changes in CTI reflected changes in species abundance in the two regions. The pattern of changes in species abundance in southwest Britain relative to their thermal affinities (STIs) produced CTI changes that were consistent with a shift towards a community dominated by cold-affinity species: CTI for animal species and CTI for plants and algae decreased from 2002 to 2018. The reduced response of CTI to temperature change in Shetland was associated with an inconsistent pattern of abundance change among species. Plants and algae in Shetland had a much smaller spread of STIs (0.93°C, Table S7) than in southwest Britain (2.48°C), while animals in Shetland (2.38 °C) were also less thermally diverse than in southwest Britain (4.63 °C). Thermal ranges were similar in both regions.

Discussion

Implications of spatial patterns in community thermal diversity and range for community sensitivity to climate change

Patterns of community thermal metrics across regions and taxonomic groups allow evaluation of general predictions of the sensitivity of community thermal composition to temperature change. Negative thermal bias, where the community is dominated by cold-affinity species and potentially vulnerable to the effects of warming (Stuart-Smith *et al.*, 2015), was seen for communities of macroalgae across most of the UK, increasing from eastern Scotland and northeast England towards southwest Britain and Ireland (Fig. 2b). This suggests potentially greater negative effects of climate warming on intertidal macroalgae in the southwest of the UK. Changes in abundance of large brown algae in the UK over recent times may match this expectation, with declines in abundance with warming in the southern half of the UK and no changes in central and northern regions (Yesson *et al.*, 2015). Trends in abundance of macroalgae in southwest Britain since 2002 show the opposite trend, with macroalgae increasing during a period of stasis or slight cooling, but remain consistent with the general expectation of "thermophilization" during warming

and its opposite during cooling. The pattern of increase in macroalgae in Shetland since 1976 was not consistent with this idea, with a decline in macroalgae CTI despite the marked warming suggesting other causes for the increase in cold-affinity fucoids. Communities of intertidal animals, by contrast, have mostly positive thermal bias across the study region (Fig. 2a), suggesting that intertidal animals may benefit from the effects of warming since, on average, they have distributions centred in warmer areas. Warm-affinity animal species declined with cooling in the southwest, but the main contribution to changing CTI in Shetland was the decline in cold-affinity animals with warming.

Communities with more widely varying species thermal affinities (lower CTDiv) have been predicted to have CTI values that are more sensitive to change in environmental temperature (Burrows *et al.*, 2019), since they are more likely to show change in species relative abundance. Here, animal communities are markedly more thermally diverse than plant communities in both regions with time series, and in both regions CTI for animal communities responded more to temperature increase than CTI for plant communities. Thus, communities in southwest England and Wales that are comprised of a mix of lusitanian and boreal species are more likely to show changes: biogeographic transition zones may be "hotspots" for observing climate-related shifts in community composition. Among sites in southwest Britain, trends were not related to relatively small differences in CTDiv and CTR. Greater change in community composition was expected at wave-exposed sites, since wave-sheltered sites have been considered as stable and characterised by long-lived species such as *Ascophyllum nodosum* (Lewis, 1976). A slower or delayed response to temperature, associated with dominance by longer-lived species is suggested by the greater temporal autocorrelation of the Shetland CTI time series (Table 2).

CTI response to temperature change

The period of stable and slight cooling of sea temperatures in southwest Britain followed a period of more positive trend in temperatures the mid-1980s to 2000 (Fig. S3), during which much of the change in distribution of species since the 1960s reported at the start of the MarClim programme occurred (Herbert *et al.*, 2003, Mieszkowska *et al.*, 2014b, Simkanin *et al.*, 2005). Despite the weak response to annual changes in average annual sea surface temperature, compositional changes shown by CTI were broadly in line with the longer-term trend in temperature in both southwest Britain and Shetland. Species may be responding to other aspects of temperature change, and these responses are taxon-specific. Cold-affinity species may proliferate, for example, for reasons other than temperature such as locally enhanced food supply for suspension feeders (Burrows, 2012), or due to indirect effects including changes in trophic interactions (Russell *et al.*, 2013). The spatial pattern of CTI for animals is better aligned to the

east-west gradient of winter temperatures across the UK and Ireland, while CTI for plants better matches the north-south gradient of summer temperatures, suggesting the limiting processes may occur in different seasons for the two groups. Seawater temperatures are more important than air temperatures at setting geographical limits for intertidal limpets (Seabra *et al.*, 2016) but air temperatures may have greater effects on macroalgae, for which desiccation and osmotic stress may be more important (Davison & Pearson, 1996). In Portugal ranges of cold-affinity algae expanded towards warmer water despite apparent warming (Lima *et al.*, 2007), potentially due to the modification of inshore temperatures by upwelling. In UK regional seas, cold-affinity fucoids showed damage during hot summers due to tide-out stress particularly high on the shore (2018, personal observations, and 1983/84, Hawkins & Hartnoll, 1985). Contrary range responses in macroalgae suggest that other species traits may be shared among species with similar thermal affinities, generating compositional changes that result in CTI change (Bowler *et al.*, 2017). Intertidal macroalgae may be sensitive to changes in coastal light attenuation, with reduced abundance in areas of increased coastal phytoplankton around the UK (Burrows *et al.*, 2008). Phytoplankton increased over the region since the early 1970s (Reid *et al.*, 2001), making reduced light an unlikely cause.

Interactions as an influence on community composition response to warming

In an analogous way to forest vegetation (De Frenne *et al.*, 2013), loss of canopy may exacerbate / accelerate community change on temperate rocky shores, since canopies confer shelter. Patterns of CTI for animals across wave exposure suggest facilitation of cold-affinity animal species (e.g. *Semibalanus*) by canopy macroalgae (Bertness & Leonard, 1997)(e.g. *Fucus vesiculosus*) on wave-sheltered shores, particularly towards range limits (and potentially higher on the shore). While sweeping by macroalgae may negatively affect some species under seaweed canopies in wave exposed places (Hawkins, 1983), seaweed canopies may protect organisms living on the rock surface from the direct heating effects of sunlight and from desiccation during tide-out periods, allowing cold-affinity species to thrive at higher average temperatures than otherwise would be possible. In-situ data loggers show that temperatures under algal canopies are up to 5°C lower than on exposed rock (Moore *et al.*, 2007, Pocklington *et al.*, 2018). Thus decline and loss of macroalgae through warming, made more likely by negative thermal bias of macroalgal communities across the UK, may accelerate change in animal communities towards warm-affinity species as the protective canopy effect is removed. Experimental evidence suggests that lost structural canopies may take many years to return *(Ascophyllum nodosum*, Jenkins *et al.*, 2004, Petraitis & Dudgeon, 1999).

For strongly competing species such as barnacles, decline of a cold–affinity competitive dominant (*Semibalanus balanoides*) during warming can increase warm-affinity competitively inferior species (*Chthamalus montagui*, Poloczanska *et al.*, 2008, Wethey, 1984). Other species interactions, such as predation, may also modify climatic abundance responses, though no species pairs immediately emerge from this analysis: rates of change in abundance in relation to temperature and over time more closely follow their STIs than the changes in interacting species. Species interactions may only act locally to modify abundance patterns set at larger geographical scales. Cold-affinity macroalgae may counter-intuitively increase during warming (Lima *et al.*, 2007) if their more susceptible cold-affinity grazers also decline, causing a reduction in grazing pressure (Coleman *et al.*, 2006, Jenkins *et al.*, 2005). Likewise, removal of intertidal canopy may promote the expansion of warm-affinity species (Hawkins & Harkin, 1985).

Physical microclimate as a further modifier of community response

Physically induced spatial heterogeneity in temperatures (during emersion) on intertidal shores, with crevices, steep rock faces and boulders, may also offer local microclimates that buffer the effects of warming (Helmuth *et al.*, 2006), where increase in temperature may reduce the amount of suitably cool habitat for cold-affinity species (Denny *et al.*, 2011). Intertidal shores offer vertical temperature gradients too, with some warm-affinity species increasingly restricted to warmer, higher levels towards their cold range boundaries (Crisp *et al.*, 1981). Proximity of areas of lower temperatures may reduce the velocity of climate change in an area and thereby the associated climatic debt (Gaüzère *et al.*, 2017): changes in temperature are easily accommodated by small-scale shifts in distributions (disappearance from open rock/high shore). Most of these arguments apply to conditions in the intertidal during exposure to the air; those species limited by in-affinity temperatures have no easy escape. Small-scale oceanographic features such as tidal mixing fronts (Pingree & Griffiths, 1978) or local upwelling (Menge & Menge, 2013) may contribute to local-scale variation in community composition among survey sites for such species.

Broader implications

Our study shows that community composition on rocky shores, as average species thermal affinity, does track changes in coastal sea temperature over time, especially over longer periods, during periods of both warming and cooling. Much climate-related change is occurring beside shifting species' range margins, with likely effects of changes in population abundances and relative dominance of species on the functioning of ecosystems, including the structure of marine food webs (Serpetti *et al.*, 2017). These large spatial patterns and long-term changes in communities are consistent with the expectation that climate-driven changes in abundance are related to the thermal affinity of the constituent species compared with local temperatures, evident over long-term

changes in shelf fishes (Morley *et al.*, 2017, Simpson *et al.*, 2011), but also in species responses to heatwaves (Smale *et al.*, 2019). Combined with a greater integration with understanding of *in situ* species-level physiological response to temperature (Sinclair *et al.*, 2016), this approach offers the prospect of strong predictive power as to the direction of community compositional change in relation to climate in response to anthropogenic warming.

References

Bates AE, Bird TJ, Stuart-Smith RD *et al.* (2015) Distinguishing geographical range shifts from artefacts of detectability and sampling effort. *Diversity and Distributions,* **21**, 13-22.

Bertness MD, Leonard GH (1997) The role of positive interactions in communities: lessons from intertidal habitats. *Ecology,* **78**, 1976-1989.

Bonachela JA, Burrows MT, Payne MR, Pinsky ML (2019) Rate of community response to climate change depends on species traits and community composition. *Ecology Letters,* **in review**.

Bowler DE, Hof C, Haase P *et al.* (2017) Cross-realm assessment of climate change impacts on species' abundance trends. *Nature Ecology & Evolution,* **1**, 0067.

Breeman A (1988) Relative importance of temperature and other factors in determining geographic boundaries of seaweeds: experimental and phenological evidence. *Helgoländer Meeresuntersuchungen,* **42**, 199.

Burrows MT (2012) Influences of wave fetch, tidal flow and ocean colour on subtidal rocky communities. *Marine Ecology Progress Series,* **445**, 193-207.

Burrows MT, Bates AE, Costello MJ *et al.* (2019) Ocean community warming responses explained by thermal affinities and temperature gradients. *Nature Climate Change,* **in press**.

Burrows MT, Harvey R, Robb L (2008) Wave exposure indices from digital coastlines and the prediction of rocky shore community structure. *Marine Ecology Progress Series,* **353**, 1-12.

Burrows MT, Moore JJ, James B (2002) Spatial synchrony of population changes in rocky shore communities in Shetland. *Marine Ecology Progress Series,* **240**, 39-48.

Burrows MT, Schoeman DS, Buckley LB *et al.* (2011) The pace of shifting climate in marine and terrestrial ecosystems. *Science,* **334**, 652-655.

Chamberlain S, Szocs E (2013) taxize - taxonomic search and retrieval in R. *F1000Research*.

Cheung WWL, Watson R, Pauly D (2013) Signature of ocean warming in global fisheries catch. *Nature,* **497**, 365-368.

406 Coleman RA, Underwood AJ, Benedetti-Cecchi L *et al.* (2006) A continental scale evaluation of
407 the role of limpet grazing on rocky shores. *Oecologia,* **147**, 556-564.

408 Crisp DJ, Fischer-Piette E (1959) Repartition des principales espèces intercotidales de la côte
409 atlantique française en 1954–1955. *Annales de l'Institut Océanographique de Monaco,* **36**,
410 275-287.

411 Crisp DJ, Southward AJ (1958) The distribution of intertidal organisms along the coasts of the
412 English Channel. *Journal of the Marine Biological Association of the United Kingdom,* **37**,
413 157-208.

414 Crisp DJ, Southward AJ, Southward EC (1981) On the distribution of the intertidal barnacles
415 *Chthamalus stellatus*, *Chthamalus montagui* and *Euraphia depressa*. *Journal of the Marine*
416 *Biological Association of the United Kingdom,* **61**, 359-380.

417 Davison IR, Pearson GA (1996) Stress tolerance in intertidal seaweeds. *Journal of Phycology,* **32**,
418 197-211.

419 De Frenne P, Rodríguez-Sánchez F, Coomes DA *et al.* (2013) Microclimate moderates plant
420 responses to macroclimate warming. *Proceedings of the National Academy of Sciences,* **110**,
421 18561-18565.

422 Denny MW, Dowd WW, Bilir L, Mach KJ (2011) Spreading the risk: small-scale body temperature
423 variation among intertidal organisms and its implications for species persistence. *Journal of*
424 *Experimental Marine Biology and Ecology,* **400**, 175-190.

425 Devictor V, Julliard R, Couvet D, Jiguet F (2008) Birds are tracking climate warming, but not fast
426 enough. *Proceedings of the Royal Society of London B: Biological Sciences,* **275**, 2743-
427 2748.

428 Devictor V, Van Swaay C, Brereton T *et al.* (2012) Differences in the climatic debts of birds and
429 butterflies at a continental scale. *Nature Climate Change,* **2**, 121.

430 Firth LB, White FJ, Schofield M *et al.* (2016) Facing the future: the importance of substratum
431 features for ecological engineering of artificial habitats in the rocky intertidal. *Marine and*
432 *Freshwater Research,* **67**, 131-143.

433 Fischer-Piette E (1936) Études sur la biogéographie intercôtidale des deux rives de la Manche.
434 *Journal of the Linnaean Society (Zoology),* **40**, 181-272.

435 Flanagan PH, Jensen OP, Morley JW, Pinsky ML (2018) Response of marine communities to local
436 temperature changes. *Ecography*.

Gaüzère P, Princé K, Devictor V (2017) Where do they go? The effects of topography and habitat diversity on reducing climatic debt in birds. *Global Change Biology,* **23**, 2218-2229.

Genner MJ, Sims DW, Wearmouth VJ, Southall EJ, Southward AJ, Henderson PA, Hawkins SJ (2004) Regional climatic warming drives long-term community changes of British marine fish. *Proceedings of the Royal Society of London Series B-Biological Sciences,* **271**, 655-661.

Givan O, Edelist D, Sonin O, Belmaker J (2018) Thermal affinity as the dominant factor changing Mediterranean fish abundances. *Global Change Biology,* **24**, e80-e89.

Hawkins SJ (1983) Interactions of *Patella* and macroalgae with settling *Semibalanus balanoides* (L.). *Journal of Experimental Marine Biology and Ecology,* **71**, 55-72.

Hawkins SJ, Harkin E (1985) Preliminary canopy removal experiments in algal dominated communities low on the shore and in the shallow subtidal on the Isle of Man. *Botanica Marina,* **28**, 223-230.

Hawkins SJ, Hartnoll RG (1985) Factors determining the upper limits of intertidal canopy-forming algae. *Marine Ecology Progress Series,* **20**, 265-271.

Hawkins SJ, Sugden HE, Mieszkowska N *et al.* (2009) Consequences of climate-driven biodiversity changes for ecosystem functioning of North European rocky shores. *Marine Ecology Progress Series,* **396**, 245-259.

Helmuth B, Broitman BR, Blanchette CA *et al.* (2006) Mosaic patterns of thermal stress in the rocky intertidal zone: Implications for climate change. *Ecological Monographs,* **76**, 461-479.

Herbert RJH, Hawkins SJ, Sheader M, Southward AJ (2003) Range extension and reproduction of the barnacle *Balanus perforatus* in the eastern English Channel. *Journal of the Marine Biological Association of the UK,* **83**, 73-82.

Hiscock K (1981) The rocky shore ecology of Sullom Voe. *Proceedings of the Royal Society of Edinburgh Section B,* **80**, 219-240.

Hutchins LW (1947) The bases for temperature zonation in geographical distribution. *Ecological Monographs,* **17**, 325-335.

Jenkins SR, Coleman RA, Della Santina P, Hawkins SJ, Burrows MT, Hartnoll RG (2005) Regional scale differences in the determinism of grazing effects in the rocky intertidal. *Marine Ecology Progress Series,* **287**, 77-86.

Jenkins SR, Norton TA, Hawkins SJ (2004) Long term effects of *Ascophyllum nodosum* canopy removal on mid shore community structure. *Journal of the Marine Biological Association of the UK,* **84**, 327-329.

Jones SJ, Southward AJ, Wethey DS (2012) Climate change and historical biogeography of the barnacle Semibalanus balanoides. *Global Ecology and Biogeography,* **21**, 716-724.

Lewis JR (1964) *The Ecology of Rocky Shores*, English Universities Press London.

Lewis JR (1976) Long-term ecological surveillance: practical realities in the rocky littoral. *Oceanography and Marine Biology: an Annual Review,* **14**, 371-390.

Lima FP, Ribeiro PA, Queiroz N, Hawkins SJ, Santos AM (2007) Do distributional shifts of northern and southern species of algae match the warming pattern? *Global Change Biology,* **13**, 2592-2604.

Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD (2009) The velocity of climate change. *Nature,* **462**, 1052-1055.

Maclean I, Hopkins JJ, Bennie J, Lawson CR, Wilson RJ (2015) Microclimates buffer the responses of plant communities to climate change. *Global Ecology and Biogeography,* **24**, 1340-1350.

Menge BA, Menge DNL (2013) Dynamics of coastal meta-ecosystems: the intermittent upwelling hypothesis and a test in rocky intertidal regions. *Ecological Monographs,* **83**, 283.

Mieszkowska N, Burrows MT, Pannacciulli FG, Hawkins SJ (2014a) Multidecadal signals within co-occuring intertidal barnacles *Semibalanus balanoides* and *Chthamalus* spp. linked to the Atlantic Multidecadal Oscillation. *Journal of Marine Systems,* **133**, 70-76.

Mieszkowska N, Firth L, Bentley M (2013) Impacts of climate change on intertidal habitats. *Marine Climate Change Impacts Partnership: Science Review,* **4**, 180-192.

Mieszkowska N, Kendall M, Hawkins S, Leaper R, Williamson P, Hardman-Mountford N, Southward A (2006a) Changes in the range of some common rocky shore species in Britain – a response to climate change? *Hydrobiologia,* **555**, 241-251.

Mieszkowska N, Leaper R, Moore P *et al.* (2006b) Marine biodiversity and climate change assessing and predicting the influence of climatic change using intertidal rocky shore biota. *Scottish Natural Heritage Commissioned Report No. 202 (ROAME No. F01AA402)*, 1-53.

Mieszkowska N, Sugden H, Firth L, Hawkins S (2014b) The role of sustained observations in tracking impacts of environmental change on marine biodiversity and ecosystems.

Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences, **372**, 20130339.

Moore P, Hawkins SJ, Thompson RC (2007) Role of biological habitat amelioration in altering the relative responses of congeneric species to climate change. *Marine Ecology Progress Series,* **334**, 11-19.

Morley JW, Batt RD, Pinsky ML (2017) Marine assemblages respond rapidly to winter climate variability. *Global Change Biology,* **23**, 2590–2601.

Petraitis PS, Dudgeon SR (1999) Experimental evidence for the origin of alternative communities on rocky intertidal shores. *Oikos*, 239-245.

Pingree RD, Griffiths DK (1978) Tidal fronts on the shelf seas around the British Isles. *Journal of Geophysical Research,* **83**, 4615-4622.

Pinheiro J, Bates D, Debroy S, Sarkar D, Team RC (2018) *nlme: Linear and Nonlinear Mixed Effects Models*.

Pocklington JB, Jenkins SR, Bellgrove A, Keough MJ, O'hara TD, Masterson-Algar PE, Hawkins SJ (2018) Disturbance alters ecosystem engineering by a canopy-forming alga. *Journal of the Marine Biological Association of the United Kingdom,* **98**, 687-698.

Poloczanska ES, Brown CJ, Sydeman WJ *et al.* (2013) Global imprint of climate change on marine life. *Nature Climate Change,* **3**, 919-925.

Poloczanska ES, Hawkins SJ, Southward AJ, Burrows MT (2008) Modeling the response of populations of competing species to climate change. *Ecology,* **89**, 3138-3149.

Princé K, Zuckerberg B (2015) Climate change in our backyards: the reshuffling of North America's winter bird communities. *Global Change Biology,* **21**, 572.

Reid PC, Holliday NP, Smyth TJ (2001) Pulses in the eastern margin current and warmer water off the north west European shelf linked to North Sea ecosystem changes. *Marine Ecology Progress Series,* **215**, 283-287.

Reynolds RW, Rayner NA, Smith TM, Stokes DC, Wang W (2002) An improved in situ and satellite SST analysis for climate. *Journal of Climate,* **15**, 1609-1625.

Reynolds RW, Smith TM, Liu C, Chelton DB, Casey KS, Schlax MG (2007) Daily high-resolution-blended analyses for sea surface temperature. *Journal of Climate,* **20**, 5473-5496.

Russell BD, Connell SD, Findlay HS, Tait K, Widdicombe S, Mieszkowska N (2013) Ocean acidification and rising temperatures may increase biofilm primary productivity but decrease grazer consumption. *Phil. Trans. R. Soc. B,* **368**, 20120438.

Seabra R, Wethey DS, Santos AM, Gomes F, Lima FP (2016) Equatorial range limits of an intertidal ectotherm are more linked to water than air temperature. *Global Change Biology,* **22**, 3320-3331.

Seabra R, Wethey DS, Santos AM, Lima FP (2015) Understanding complex biogeographic responses to climate change. *Scientific Reports,* **5**.

Serpetti N, Baudron AR, Burrows M, Payne BL, Helaouet P, Fernandes PG, Heymans J (2017) Impact of ocean warming on sustainable fisheries management informs the Ecosystem Approach to Fisheries. *Scientific Reports,* **7**, 13438.

Simkanin C, Power A, Myers A *et al.* (2005) Using historical data to detect temporal changes in the abundances of intertidal species on Irish shores. *Journal of the Marine Biological Association of the United Kingdom,* **85**, 1329-1340.

Simpson SD, Jennings S, Johnson MP, Blanchard JL, Schön PJ, Sims DW, Genner MJ (2011) Continental shelf-wide response of a fish assemblage to rapid warming of the sea. *Current Biology*.

Sinclair BJ, Marshall KE, Sewell MA *et al.* (2016) Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecology Letters,* **19**, 1372-1385.

Smale DA, Wernberg T, Oliver ECJ *et al.* (2019) Marine heatwaves threaten global biodiversity and the provision of ecosystem services. *Nature Climate Change*, 12.

Sorte CJB, Williams SL, Carlton JT (2010) Marine range shifts and species introductions: comparative spread rates and community impacts. *Global Ecology and Biogeography,* **19**, 303-316.

Southward AJ (1991) Forty years of changes in species composition and population density of barnacles on a rocky shore near Plymouth. *Journal of the Marine Biological Association of the UK,* **71**, 495-513.

Southward AJ, Crisp DJ (1954a) The distribution of certain intertidal animals around the Irish coast. *Proceedings of the Royal Irish Academy,* **57B**, 1-29.

557 Southward AJ, Crisp DJ (1954b) Recent changes in the distribution of the intertidal barnacles
558 *Chthamalus stellatus* Poli and *Balanus balanoides* L. in the British Isles. *Journal of Animal*
559 *Ecology,* **23**, 163-177.

560 Southward AJ, Hawkins SJ, Burrows MT (1995) 70 years observations of changes in distribution
561 and abundance of zooplankton and intertidal organisms in the western English Channel in
562 relation to rising sea temperature. *Journal of Thermal Biology,* **20**, 127-155.

563 Stuart-Smith RD, Edgar GJ, Barrett NS, Kininmonth SJ, Bates AE (2015) Thermal biases and
564 vulnerability to warming in the world's marine fauna. *Nature,* **528**, 88-92.

565 Sunday JM, Bates AE, Dulvy NK (2012) Thermal tolerance and the global redistribution of
566 animals. *Nature Climate Change,* **2**, 686-690.

567 Tayleur CM, Devictor V, Gaüzère P, Jonzén N, Smith HG, Lindström Å (2016) Regional variation
568 in climate change winners and losers highlights the rapid loss of cold-dwelling species.
569 *Diversity and Distributions,* **22**, 468-480.

570 Tingley MW, Beissinger SR (2009) Detecting range shifts from historical species occurrences: new
571 perspectives on old data. *Trends in Ecology & Evolution*.

572 Wethey DS (1984) Sun and shade mediate competition in the barnacles Chthamalus and
573 Semibalanus: a field experiment. *Biology Bulletin,* **167**, 176-185.

574 Yesson C, Bush LE, Davies AJ, Maggs CA, Brodie J (2015) Large brown seaweeds of the British
575 Isles: Evidence of changes in abundance over four decades. *Estuarine, Coastal and Shelf*
576 *Science*.

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578 **Figures**

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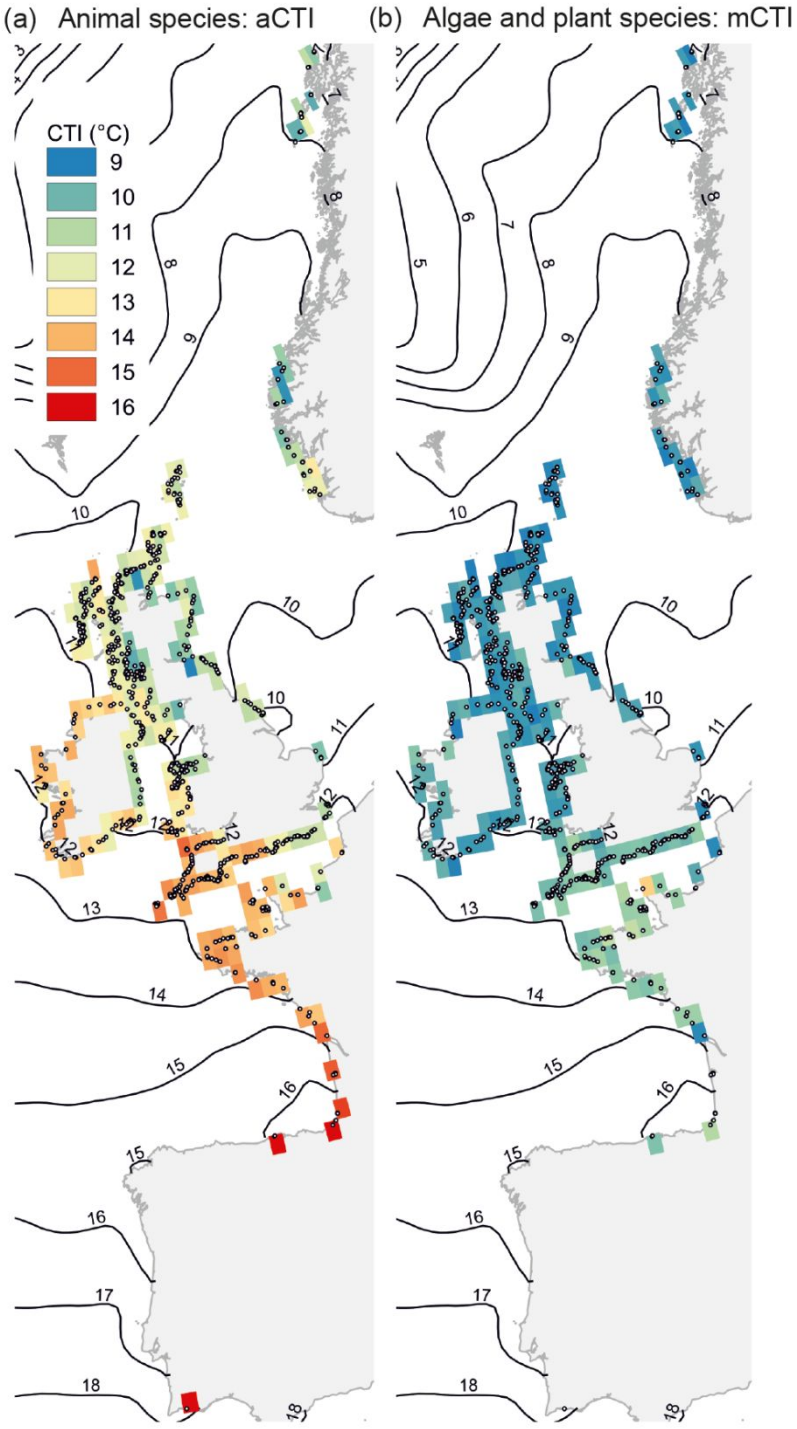

580

581 **Fig. 1** Geographical patterns in CTI for (a) animals and (b) plants and algae. Community
582 Temperature Index values are shown as averages in 0.5°-degree grid cells, with survey sites as open
583 circles. Isotherms are average annual sea surface temperature at 1°C intervals from the NOAA
584 OISSTv2 HR dataset.

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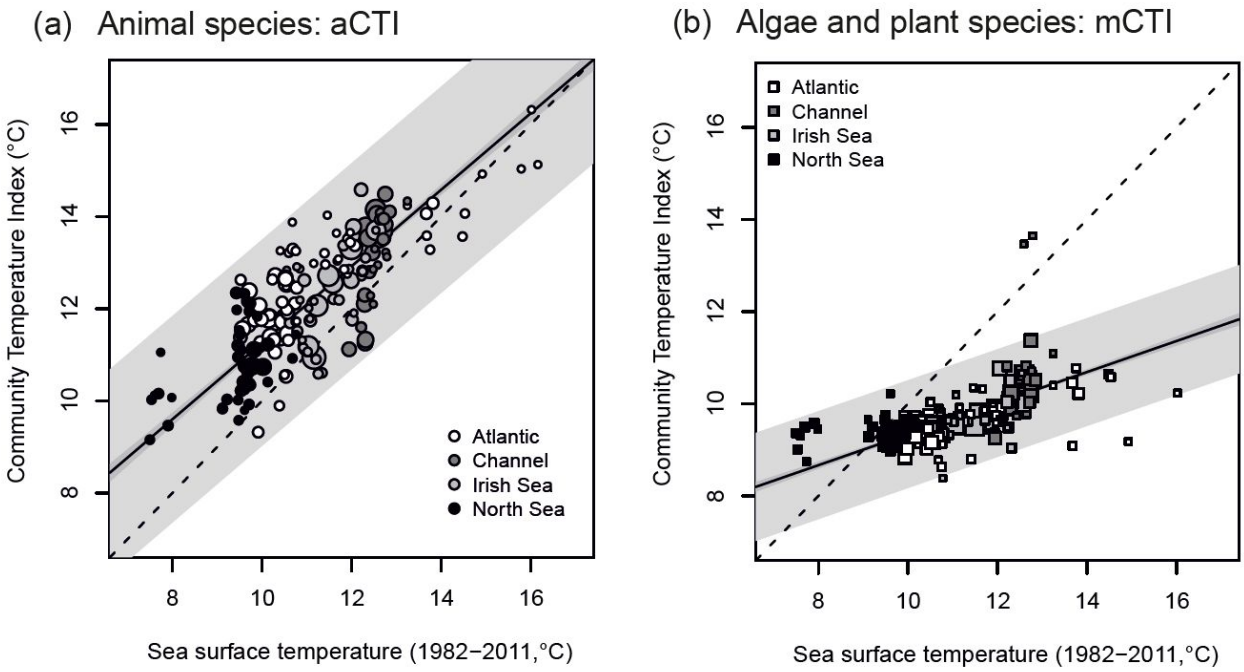

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589 **Fig. 2** Community Temperature Index versus average annual sea surface temperature. CTI for (a)
590 animal species is more sensitive to local SST (R^2 = 0.46, y= 2.75(0.22)+ 0.85(0.02)x, standard
591 errors in paretheses) than for (b) algal species (R^2 = 0.32, y= 5.94(0.12)+ 0.34(0.01)x). Solid lines
592 show regressions with 95% confidence intervals for slopes (dark grey ribbon) and predicted values
593 (light grey); dashed lines show 1:1. Symbols show mean CTI values for data aggregated into 0.5°
594 latitude-longitude cells with symbol size indicating the number of sites in each cell and shading
595 denoting coastlines.

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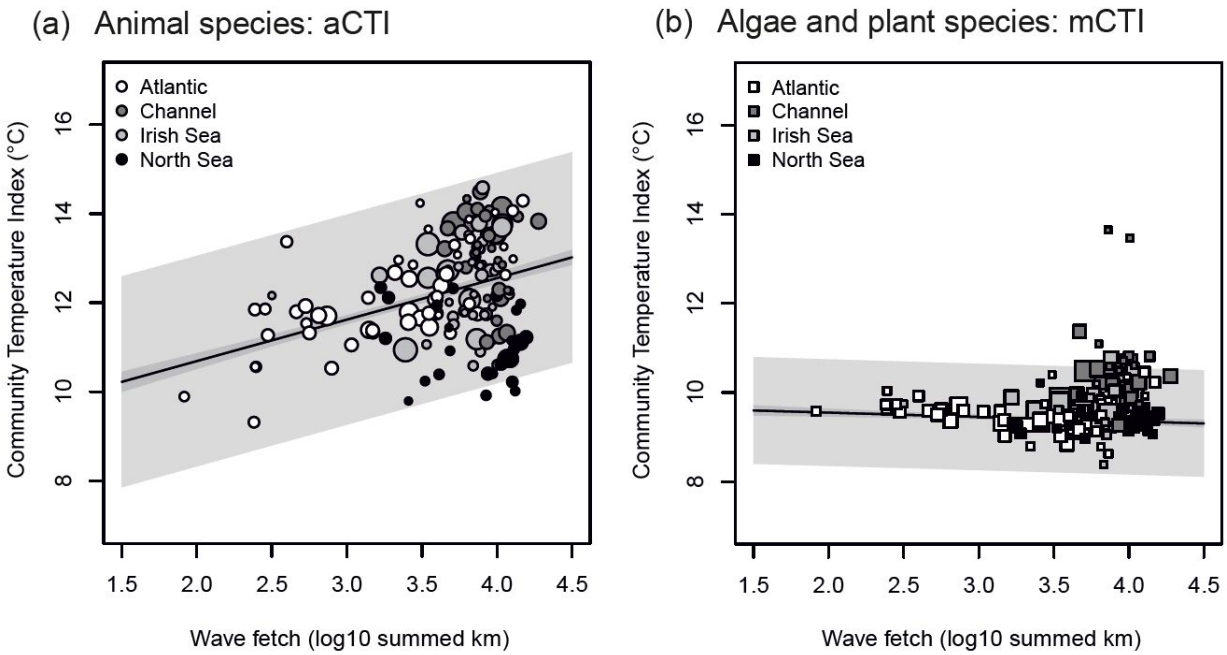

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599 **Fig. 3** (a) Animal communities in wave-sheltered conditions tend to be composed of species with
600 cooler thermal affinities than in wave-exposed conditions (R^2 = 0.36, y= 9.10(0.20) + 0.86(0.06)x +
601 region terms), a trend not seen in (b) algal communities (R^2 = 0.26, y= 9.65(0.10) - 0.07(0.03)x +
602 region terms). Solid lines show regressions with 95% confidence intervals for slopes (dark grey
603 ribbon) and predictions (light grey ribbon) for Atlantic coastal sites. Symbols show CTI values for
604 data aggregated into 0.5° latitude-longitude cells, with size indicating the number of sites in each
605 cell.

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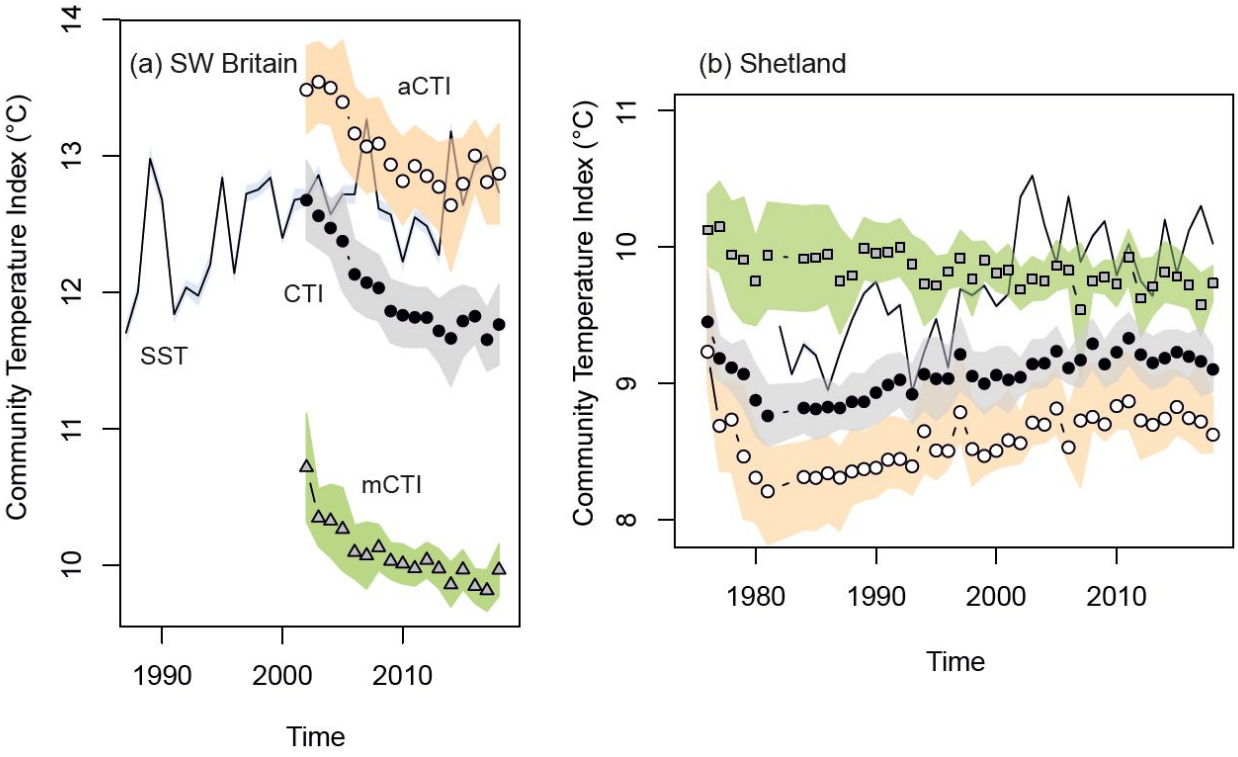

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611 **Fig. 4** Change in Community Temperature Index in (a) southwest Britain (n=40 sites) and (b)
612 Shetland (n=15 sites) as annual means across sites for all species combined (CTI, filled circles; size
613 scaled to the frequency of occurrence of species), animal species (aCTI, open circles) and plants
614 and algae (mCTI, shaded squares Shetland, triangles SW Britain). Regional sea surface
615 temperatures are shown as mean annual temperatures for each region from OISST HR V2.
616 Uncertainties are shown as 95% confidence intervals of means (shaded ribbons) of site CTI values,
617 and for SST as ranges of values in neighbouring grid cells .
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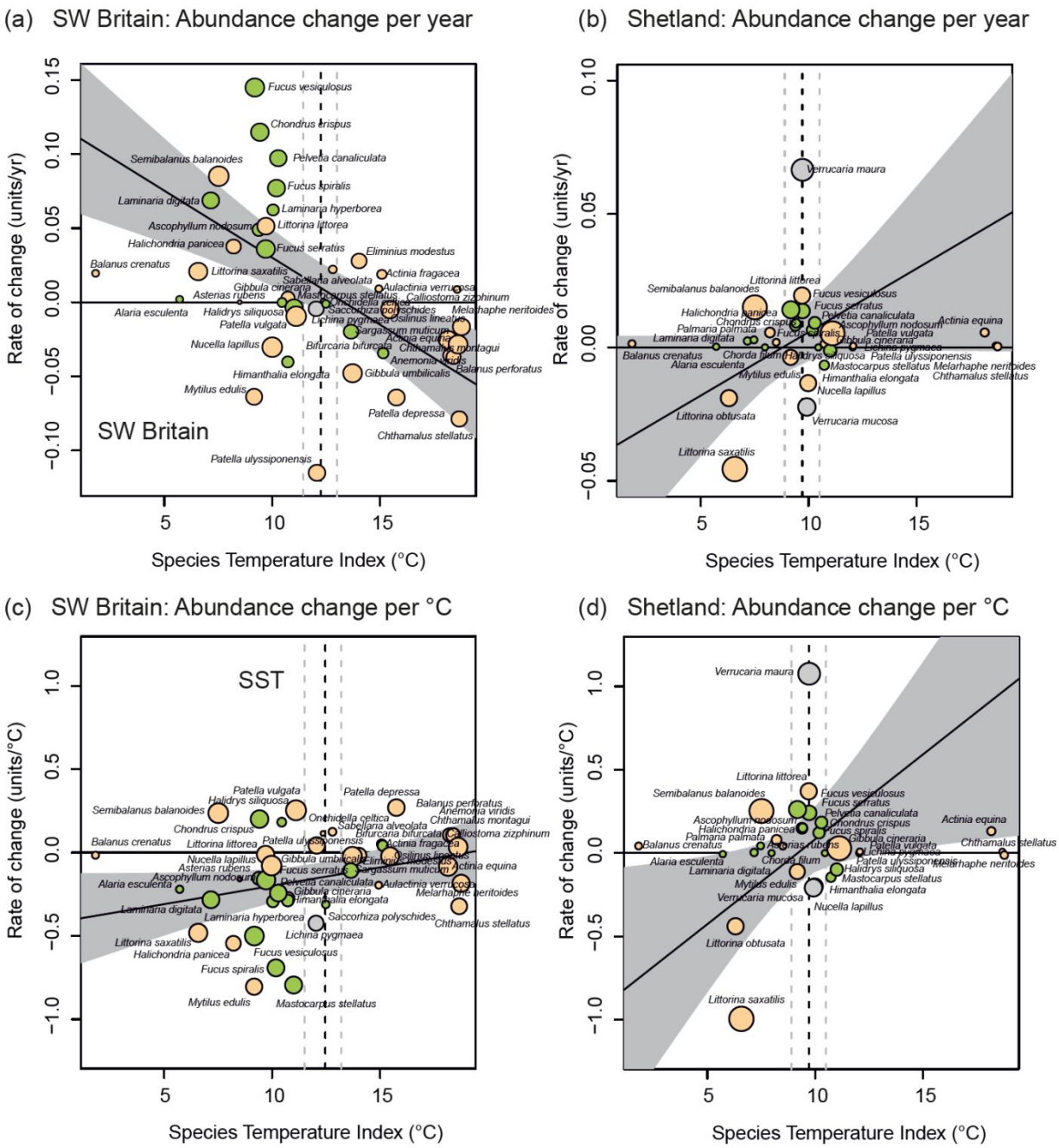

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620 **Fig. 5** Trends in species abundance in (a, c) SW Britain (2002-2018) and (b, c) Shetland (1984-
621 2018) related to species thermal affinities (Species Temperature Index). Each point represents the
622 regression coefficient for a single species against (a, b) regional annual SST and (c, d) years.
623 Species thermal affinities (STI) influenced trends over time in SW Britain (a, R^2=0.15, P=0.005)
624 and mariginally in Shetland (b, R^2=0.09, P=0.06). Trends with SST in were related to STI in SW
625 Britain (a, R^2=0.06, P=0.06) and Shetland (b, R^2=0.13, P=0.03). Regressions are shown by slopes
626 and their 95% confidence levels as shaded areas. Green circles, plants and algae; beige circles,
627 animals; sizes of circles scaled to proportional frequency of species, used as weighting in
628 regression. Vertical dashed lines show average (black) and range (grey) in local annual average
629 SST.

630 **Table 1** Spatial variation in thermal community composition metrics related to site-averaged values
631 with local sea surface temperature and site-specific wave exposure (log_{10} summed wave fetch).
632 Values are parameter estimates and t-values from generalised linear models with spherical spatial
633 correlation structure, using site-averaged community thermal metrics as the response variable
634 (n=912). All p-values <0.001 except §. Equivalent R^2 values shown in brackets.
635

	Estimate	SE	t		Estimate	SE	t
CTI, Community Temperature Index		(R^2 0.594)		**Species richness**			(R^2 0.076)
(Intercept)	2.96	0.233	12.72	(Intercept)	§2.703	2.266	1.19
SST	0.681	0.021	32.87	SST	0.853	0.202	4.22
Wave fetch	0.191	0.04	4.79	Wave fetch	2.305	0.390	5.91
aCTI, animal species		(R^2 0.400)		**Species richness: animals**			(R^2 0.222)
(Intercept)	3.018	0.379	7.96	(Intercept)	-18.652	2.732	-6.83
SST	0.668	0.034	19.76	SST	2.823	0.242	11.69
Wave fetch	0.512	0.065	7.87	Wave fetch	3.188	0.471	6.76
mCTI, macroalgae and plant species		(R^2 0.352)		**Species richness: macroalgae and plants**			(R^2 0.018)
(Intercept)	6.123	0.18	34	(Intercept)	15.088	1.596	9.45
SST	0.361	0.016	22.49	SST	-0.367	0.142	-2.58
Wave fetch	-0.127	0.031	-4.09	Wave fetch	1.053	0.275	3.84

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Table 2 Linear mixed models of changes in abundance-weighted CTI over time. For comparison of changes in CTI with temperature changes (CTI vs SST) random-intercepts models were fitted using regional sea surface temperature anomaly as a fixed factor and sites as a random factor. For trends in CTI over time similar models were fitted using year as a fixed factor. Temporal autocorrelation was included as a within-sites autoregressive (AR1) term. (Shetland time series: n obs=508, n sites=15, duration=41 years, 40 years surveyed but temperature available for 35 years from 1982 onwards. SW Britain time series: n obs=815, n sites=60, duration=17 years).

Shetland 1984-2018	**Fixed effects**						**Random effects**	
	Estimate	**SE**	**Estimate**	**SE**	***t***	***p***	**SD (intercept)**	**AR1 (Year)**
CTI vs SST	**(Intercept)**		**SST anomaly**					
CTI	9.078	0.085	0.133	0.028	4.784	<0.001	0.322	0.514
aCTI	8.606	0.144	0.168	0.041	4.061	<0.001	0.551	0.419
mCTI†	9.802	0.065	-0.059	0.047	-1.236	0.217	0.238	0.315
CTI vs Year			**Year**					
CTI	-12.972	2.652	0.011	0.001	8.322	<0.001	0.322	0.440
aCTI	-17.406	3.762	0.013	0.002	6.920	<0.001	0.550	0.379
mCTI	22.148	4.198	-0.006	0.002	-2.941	0.003	0.238	0.304

(nobs=508, nsites=15)

SW Britain 2002-2018	**Fixed effects**						**Random effects**	
	Estimate	**SE**	**Estimate**	**SE**	***t***	***p***	**SD**	**AR1 (Year)**
CTI vs SST	**(Intercept)**		**SST anomaly**					
CTI	11.886	0.113	0.056	0.044	1.265	0.206	0.856	0.341
aCTI	12.900	0.147	0.113	0.060	1.892	0.059	1.118	-0.102
mCTI	10.039	0.067	-0.099	0.043	-2.273	0.023	0.488	0.360
CTI vs Year			**Year**					
CTI	74.172	7.352	-0.031	0.004	-8.472	<0.001	0.838	0.241
aCTI	36.441	9.319	-0.012	0.005	-2.523	0.012	1.107	0.153
mCTI	63.449	7.534	-0.027	0.004	-7.093	<0.001	0.481	0.265

(nobs=815, nsites=60)

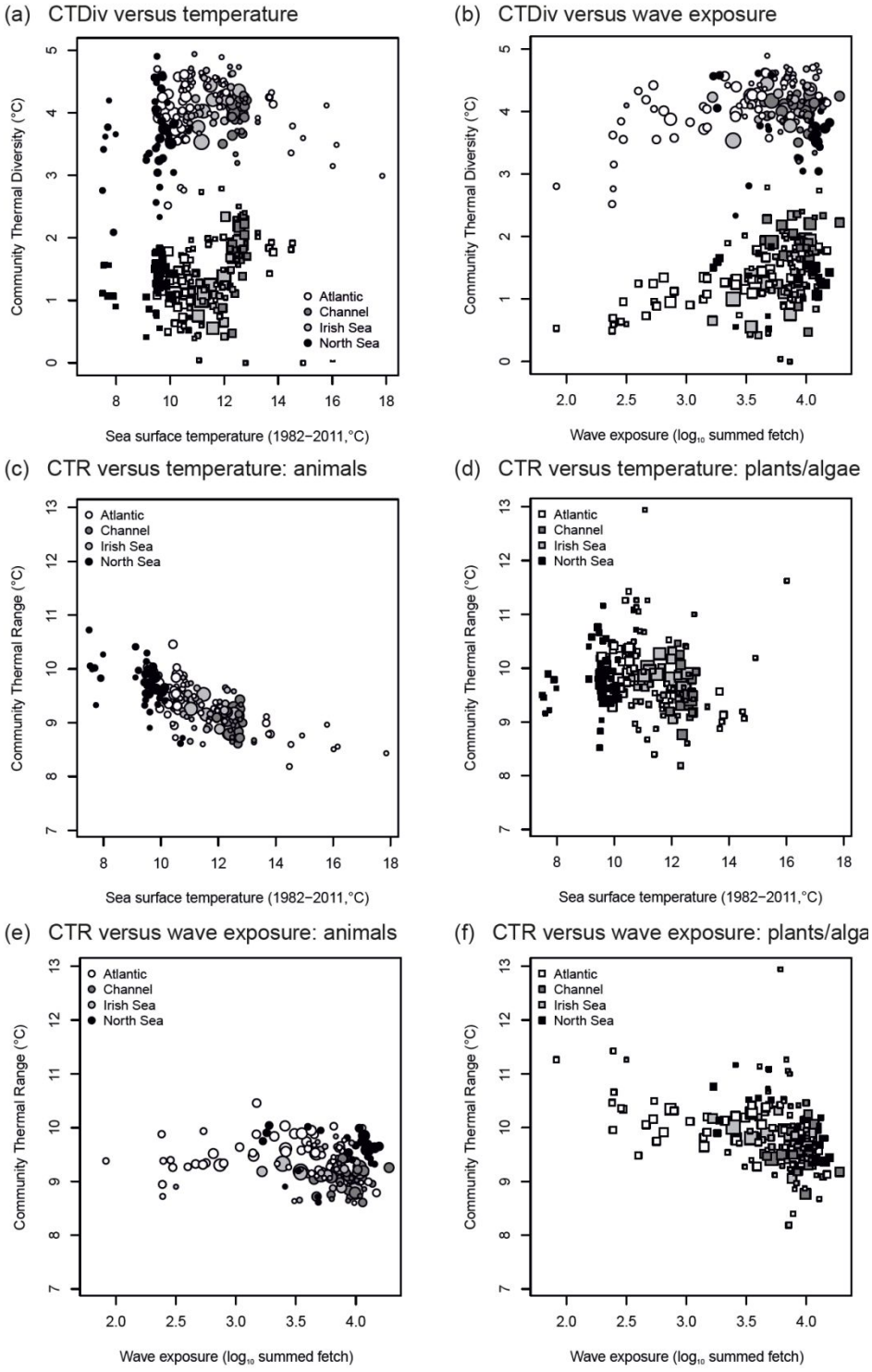


Fig. S1 Patterns in community thermal metrics across temperature and wave exposure gradients, averaged in 0.5° latitude-longitude areas. (a) Diversity of species thermal affinities (Community Thermal Diversity, CTDiv) for animal communities (circles) and (b) plant-algae communities (squares, size indicating number of sites in each area) versus sea surface temperature (SST). (c) Average species thermal range width (CTR) for animals and (d) plant-algae communities versus SST and (e, f) wave exposure.

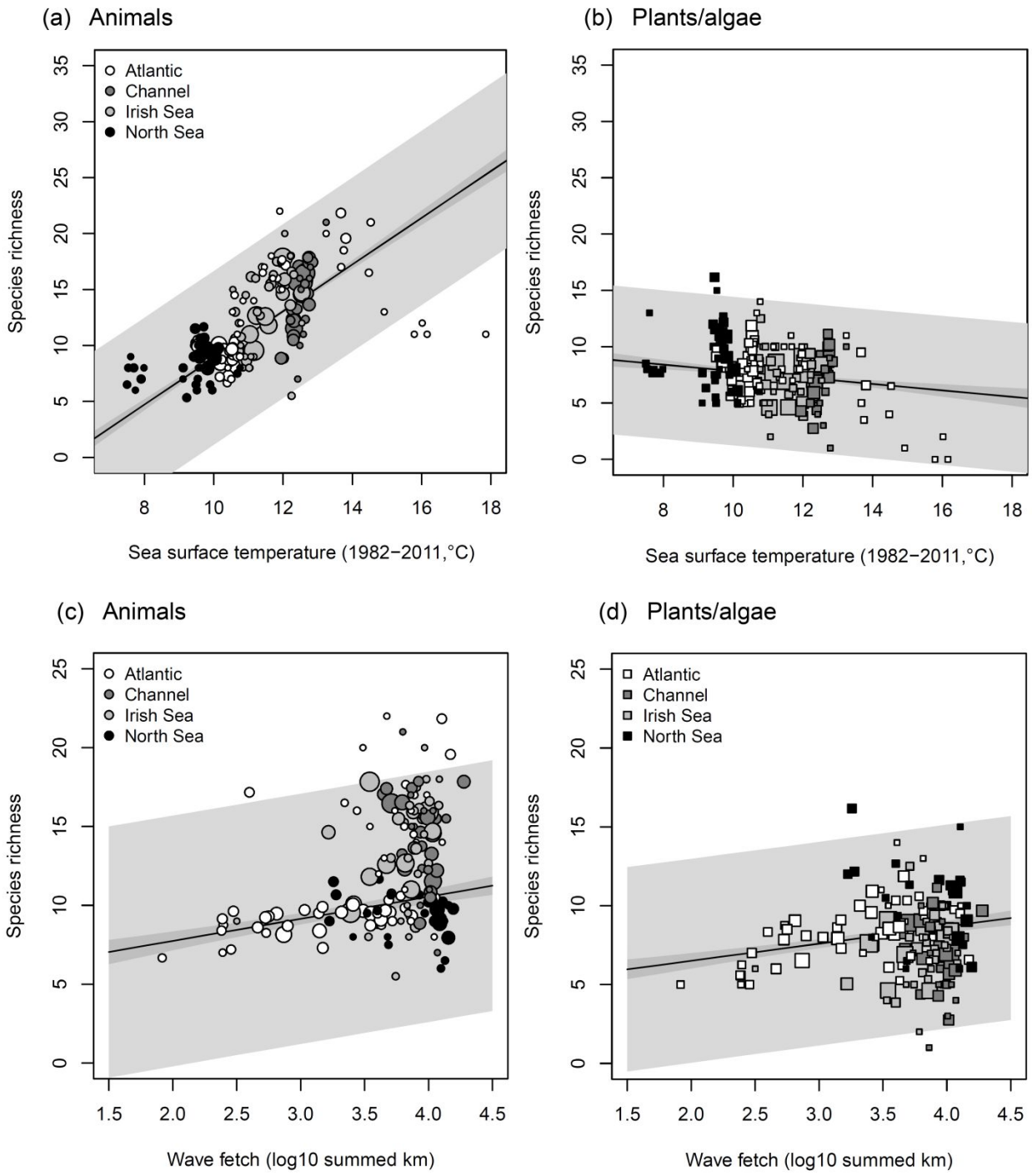
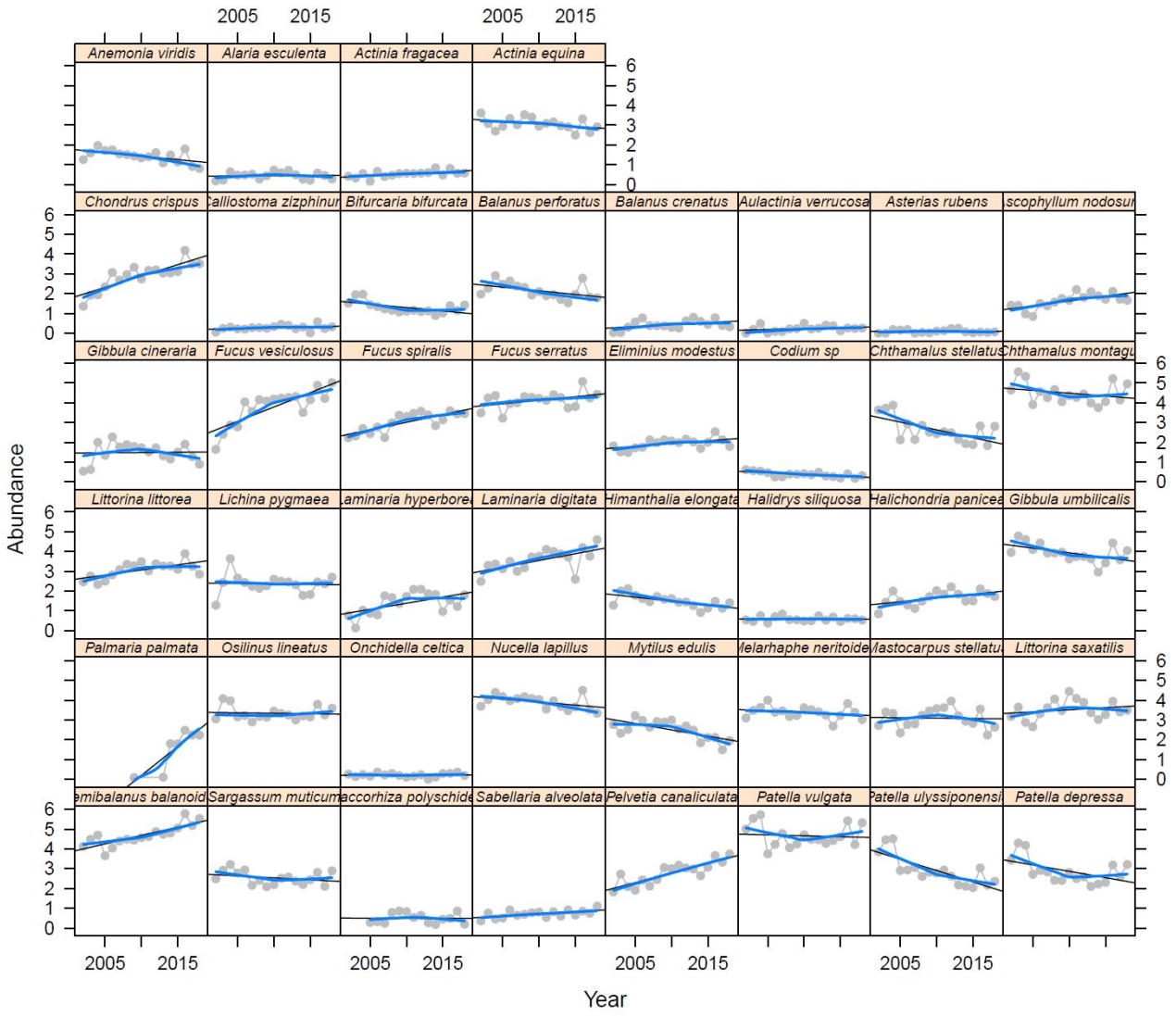


Fig. S2 Patterns in species richness for rocky-shore animal communities (a,c) and plant-algal communities across temperature (a,b) and wave exposure (c,d) gradients, averaged in 0.5° latitude-longitude areas. Symbol sizes reflect numbers of sites surveyed per 0.5° area, and symbol shading showing coastline locations. Lines show regression models: (a, c) $R^2 = 0.22$, (b, d) $R^2 = 0.08$.



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662 **Fig. S3** Changes in average abundance of predominant species in MarClim surveys across

663 frequently sampled (n visits ≥10) sites in southwest Britain from 2002 to 2018, as average values of

664 SACFORN categories expressed as integers (S:6 to N:0). In each panel the black line shows the

665 simple linear regression fit and the blue line shows a loess-smoothed regression (span=1).

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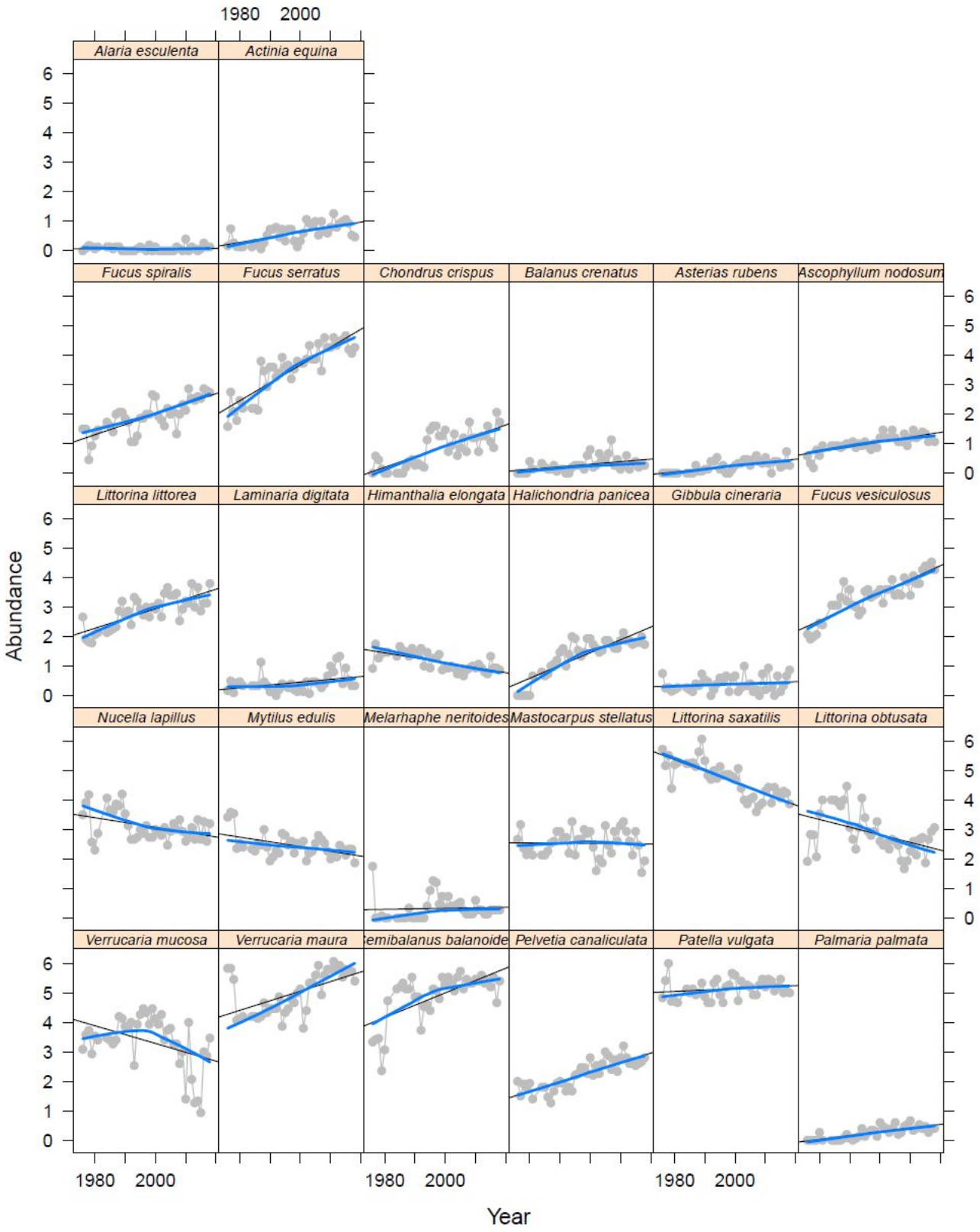

668

669 **Fig. S4** Changes in average abundance of predominant species in SOTEAG surveys at sites around
670 Sullom Voe in Shetland from 1976 to 2018, as average values of SACFORN categories expressed
671 as integers (S:6 to N:0). In each panel the black line shows the simple linear regression fit and the
672 blue line shows a loess-smoothed regression (span=1).

Table S1 Species Temperature Index (STI) values for the subset of UK rocky shore species used in CTI estimation, arranged by taxonomy. Geographical range polygons derived from literature reports and personal observations were used to extract sea surface temperatures for coastal cells from the NOAA OISST HR 0.25° dataset (Reynolds *et al.*, 2007) using average annual values for 1982 to 2011 inclusive. Thermal ranges were expressed as percentiles of the within-range set of coastal temperatures, with the STI taken as the median temperature T50 and the Species Thermal Range (STR) as the difference between the 10th and 90th percentiles (T90-T10). Numbered reference and information sources for range extents are listed in Table S2. Range polygons are available as ESRI shapefiles at doi:10.6084/m9.figshare.8284016 .

Abbr	Species1	Class	Phylum	Kingdom	T0	T10	T25	T50	T75	T90	T100	STR	Reference				
Saalv	*Sabellaria alveolata*	Polychaeta	Annelida	Animalia	10.54	11.07	11.79	12.80	15.93	17.77	19.04	6.70	58				
Bacre	*Balanus crenatus*	Hexanauplia	Arthropoda	Animalia	-1.68	-1.15	-0.71	1.82	6.39	9.96	14.56	11.10	25				
Baper	*Perforatus perforatus*	Hexanauplia	Arthropoda	Animalia	11.55	12.48	14.67	18.39	19.43	22.27	26.41	9.78	25				
Chmon	*Chthamalus montagui*	Hexanauplia	Arthropoda	Animalia	9.42	11.66	16.28	18.62	19.58	21.30	22.34	9.64	1	12	13		
Chspp	*Chthamalus species*	Hexanauplia	Arthropoda	Animalia	9.43	12.08	16.16	18.65	19.72	21.34	22.46	9.26					
Chste	*Chthamalus stellatus*	Hexanauplia	Arthropoda	Animalia	9.44	12.49	16.03	18.67	19.85	21.38	22.58	8.88	1	15	16	12	13
Elmod	*Eliminius modestus*	Hexanauplia	Arthropoda	Animalia	9.43	10.38	11.67	14.02	15.79	17.44	22.48	7.06	67	68	70		
Sebal	*Semibalanus balanoides*	Hexanauplia	Arthropoda	Animalia	-0.07	1.20	4.20	7.51	10.50	12.41	22.65	11.22	2	3	4	19	
Acequ	*Actinia equina*	Anthozoa	Cnidaria	Animalia	2.48	9.57	12.32	18.16	19.48	21.24	25.14	11.67	54	55	56	57	
Acfra	*Actinia fragacea*	Anthozoa	Cnidaria	Animalia	11.00	11.93	12.38	15.08	16.45	18.81	19.67	6.88	80	81	82	83	84
Anvir	*Anemonia viridis*	Anthozoa	Cnidaria	Animalia	9.49	11.51	15.37	18.23	19.12	19.93	21.76	8.43	64				
Auver	*Aulactinia verrucosa*	Anthozoa	Cnidaria	Animalia	9.49	10.73	12.20	14.94	18.35	20.35	21.21	9.62	82	83			
Asrub	*Asterias rubens*	Asteroidea	Echinodermata	Animalia	2.48	4.26	6.31	8.50	10.58	12.18	14.30	7.92	66				
Lemue	*Leptasterias muelleri*	Asteroidea	Echinodermata	Animalia	0.20	1.75	4.64	6.33	7.95	9.72	10.85	7.98	89				
Paliv	*Paracentrotus lividus*	Echinoidea	Echinodermata	Animalia	10.52	15.67	18.11	19.04	20.30	21.49	22.58	5.82	82	86	87		
Stdro	*Strongylocentrotus droebachiensis*	Echinoidea	Echinodermata	Animalia	-1.09	0.26	2.90	5.02	7.21	9.42	12.00	9.16	47				
Myspp	*Mytilus edulis*	Bivalvia	Mollusca	Animalia	2.84	5.00	6.40	9.17	11.31	12.74	22.65	7.73	27	28	29		
Caziz	*Calliostoma zizphinum*	Gastropoda	Mollusca	Animalia	6.77	10.30	12.83	18.56	19.65	21.39	22.58	11.09	41	63			
Gicin	*Steromphala cineraria*	Gastropoda	Mollusca	Animalia	2.88	6.99	9.51	10.73	12.48	15.76	18.81	8.78	41	40	42	43	44
Gipen	*Steromphala pennanti*	Gastropoda	Mollusca	Animalia	12.53	12.80	14.54	15.69	16.95	18.59	19.26	5.79	44	46			
Giumb	*Steromphala umbilicalis*	Gastropoda	Mollusca	Animalia	9.72	10.54	11.90	13.72	16.97	18.75	19.67	8.21	9	45			
Hatub	*Haliotis tuberculata*	Gastropoda	Mollusca	Animalia	12.68	15.40	17.41	18.98	20.31	23.65	25.14	8.24	88				
Lilit	*Littorina littorea*	Gastropoda	Mollusca	Animalia	2.48	5.59	7.12	9.70	11.90	13.74	16.96	8.15	33	35			

Abbr	Species1	Class	Phylum	Kingdom	T0	T10	T25	T50	T75	T90	T100	STR	Reference			
Limar	*Littorina mariae*	Gastropoda	Mollusca	Animalia	4.20	6.67	8.91	10.34	12.12	13.78	16.29	7.11	33			
Liobt	*Littorina obtusata*	Gastropoda	Mollusca	Animalia	-1.46	0.14	1.50	6.31	9.83	12.27	16.66	12.14	33	36	37	
Lisax	*Littorina saxatilis*	Gastropoda	Mollusca	Animalia	-0.68	0.76	1.63	6.58	10.47	13.12	19.67	12.36	33	36	37	38
Mener	*Melarhaphe neritoides*	Gastropoda	Mollusca	Animalia	8.03	11.52	15.87	18.76	19.91	21.52	25.14	10.00	32	34		
Nulap	*Nucella lapillus*	Gastropoda	Mollusca	Animalia	3.65	6.39	7.67	9.98	12.10	15.37	18.81	8.98	14			
Oncel	*Onchidella celtica*	Gastropoda	Mollusca	Animalia	9.96	10.55	11.26	12.36	15.18	16.29	18.59	5.74	78	79		
Oslin	*Phorcus lineatus*	Gastropoda	Mollusca	Animalia	11.13	11.91	12.67	15.47	18.36	19.03	19.67	7.11	6	7		
Padep	*Patella depressa*	Gastropoda	Mollusca	Animalia	11.55	12.53	13.55	15.76	18.28	19.17	19.67	6.64	8	9		
Pauly	*Patella ulyssiponensis*	Gastropoda	Mollusca	Animalia	8.75	9.57	10.50	12.07	15.22	17.54	19.67	7.97	60	61	62	
Pavul	*Patella vulgata*	Gastropoda	Mollusca	Animalia	6.01	8.37	9.74	11.11	12.66	16.00	18.81	7.63	9	10	11	
Tetes	*Testudinalia testudinalis*	Gastropoda	Mollusca	Animalia	-0.30	0.88	1.55	5.52	9.07	11.07	13.31	10.19	38	39	14	
Hapan	*Halichondria panicea*	Demospongiae	Porifera	Animalia	1.01	2.79	5.27	8.21	11.87	16.24	19.14	13.44	49			
Alesc	*Alaria esculenta*	Phaeophyceae	Ochrophyta	Chromista	-1.13	-0.21	1.59	5.72	8.23	11.01	12.81	11.22	26			
Asnod	*Ascophyllum nodosum*	Phaeophyceae	Ochrophyta	Chromista	0.20	2.75	6.05	9.39	11.73	14.56	21.21	11.81	22	23		
Bibif	*Bifurcaria bifurcata*	Phaeophyceae	Ochrophyta	Chromista	10.68	11.95	12.48	15.13	18.16	19.16	19.67	7.21	26			
Chfil	*Chorda filum*	Phaeophyceae	Ochrophyta	Chromista	-1.00	2.73	5.63	7.98	12.20	18.77	24.22	16.03	26			
Fudis	*Fucus distichus*	Phaeophyceae	Ochrophyta	Chromista	-1.18	4.75	6.43	8.08	9.51	10.53	12.30	5.78	19			
Fuser	*Fucus serratus*	Phaeophyceae	Ochrophyta	Chromista	-0.51	5.29	7.14	9.72	11.64	12.77	17.08	7.48	21	24		
Fuspi	*Fucus spiralis*	Phaeophyceae	Ochrophyta	Chromista	2.88	5.54	7.15	10.18	12.83	19.01	21.36	13.47	26			
Fuves	*Fucus vesiculosus*	Phaeophyceae	Ochrophyta	Chromista	1.21	5.03	6.98	9.18	11.64	15.22	21.36	10.19	17	18		
Hasil	*Halidrys siliquosa*	Phaeophyceae	Ochrophyta	Chromista	6.48	8.24	9.50	10.45	12.04	12.67	16.08	4.43	26			
Hielo	*Himanthalia elongata*	Phaeophyceae	Ochrophyta	Chromista	6.29	7.91	9.54	10.73	12.40	15.09	16.93	7.18	26			
Ladig	*Laminaria digitata*	Phaeophyceae	Ochrophyta	Chromista	-0.58	1.11	3.59	7.17	9.61	11.27	12.81	10.17	26			
Lahyp	*Laminaria hyperborea*	Phaeophyceae	Ochrophyta	Chromista	4.20	6.04	8.08	10.04	11.94	12.74	15.57	6.71	26			
Laoch	*Laminaria ochroleuca*	Phaeophyceae	Ochrophyta	Chromista	12.30	12.70	14.61	16.02	18.14	18.77	19.59	6.07	77			
Lasac	*Saccharina latissima*	Phaeophyceae	Ochrophyta	Chromista	-1.53	0.11	3.67	6.98	9.61	11.66	15.73	11.55	26			
Pecan	*Pelvetia canaliculata*	Phaeophyceae	Ochrophyta	Chromista	2.48	5.28	8.09	10.29	12.17	15.06	17.04	9.78	20			
Sapol	*Saccorhiza polyschides*	Phaeophyceae	Ochrophyta	Chromista	8.03	9.51	10.53	12.49	16.85	19.02	20.05	9.51	26			
Samut	*Sargassum muticum*	Phaeophyceae	Ochrophyta	Chromista	6.70	9.58	11.03	13.65	17.65	20.58	24.22	11.00	71	72	73	
Vemau	*Verrucaria maura*	Eurotiomycetes	Ascomycota	Fungi	1.41	6.92	8.07	9.72	11.54	12.82	16.68	5.90	82	91	92	93

Abbr	Species1	Class	Phylum	Kingdom	T0	T10	T25	T50	T75	T90	T100	STR	Reference			
Vemuc	*Verrucaria mucosa*	Eurotiomycetes	Ascomycota	Fungi	1.74	6.41	8.08	9.92	11.71	12.70	15.39	6.29	31	90		
Lipyg	*Lichina pygmaea*	Lichinomycetes	Ascomycota	Fungi	9.42	9.83	10.60	12.04	13.74	16.05	18.54	6.22	30			
Chcri	*Chondrus crispus*	Florideophyceae	Rhodophyta	Plantae	2.84	5.57	7.03	9.42	11.33	12.66	17.87	7.09	26			
Cooff	*Corallina officinalis*	Florideophyceae	Rhodophyta	Plantae	1.21	4.50	6.63	10.10	14.74	19.14	22.31	14.64	26	74	75	76
Maste	*Mastocarpus stellatus*	Florideophyceae	Rhodophyta	Plantae	4.20	7.11	9.15	11.00	15.09	19.08	21.36	11.97	50	51	52	53
Papal	*Palmaria palmata*	Florideophyceae	Rhodophyta	Plantae	-0.58	3.01	5.47	7.47	10.01	12.01	15.57	8.99	26			

Table S2 Literature sources for global distributions of selected UK rocky shore species used for Species Temperature Index estimation. ID numbers show sources referenced in Table S1

ID	Reference
1	Crisp, D. J., A. J. Southward, and E. C. Southward. 1981. On the distribution of the intertidal barnacles *Chthamalus stellatus*, *Chthamalus montagui* and *Euraphia depressa*. Journal of the Marine Biological Association of the United Kingdom 61:359–380.
2	Barnes, H. 1957. The northern limits of *Balanus balanoides* (L). Oikos 8:1–15.
3	Wethey, D. S., and S. A. Woodin. 2008. Ecological hindcasting of biogeographic responses to climate change in the European intertidal zone. Hydrobiologia 606:139–151.
4	Wethey, D. S., S. A. Woodin, T. J. Hilbish, S. J. Jones, F. P. Lima, and P. M. Brannock. 2011. Response of intertidal populations to climate: effects of extreme events versus long term change. Journal of Experimental Marine Biology and Ecology 400:132–144.
5	Jones, S. J., A. J. Southward, and D. S. Wethey. 2012. Climate change and historical biogeography of the barnacle *Semibalanus balanoides*. Global ecology and biogeography 21:716–724.
6	Mieszkowska, N., S. J. Hawkins, M. T. Burrows, and M. A. Kendall. 2007. Long-term changes in the geographic distribution and population structures of *Osilinus lineatus* (Gastropoda : Trochidae) in Britain and Ireland. Journal of the Marine Biological Association of the United Kingdom 87:537–545.
7	Lewis, J. R. 1964. The Ecology of Rocky Shores. English Universities Press London.
8	Burrows, M. T., Moore, P., and Hawkins, S.J. 2006. Recommendations for intertidal biodiversity surveillance. Report to the Joint Nature Conservation Committee from the Marine Biological Association. Plymouth: Marine Biological Association. JNCC Contract F90-01-893.
9	http://www.mba.ac.uk/marclim/pdf/european_distribution_of_species.pdf
10	http://www.marlin.ac.uk/specieshabitats.php?speciesID=4050
11	Lewis, J. R., R. S. Bowman, M. A. Kendall, and P. Williamson. 1982. Some geographical components in population dynamics: Possibilities and realities in some littoral species. Netherlands Journal of Sea Research 16:18–28.
12	Hawkins, S. J., H. Corte-Real, F. G. Pannacciulli, L. C. Weber, and J. D. D. Bishop. 2000. Thoughts on the ecology and evolution of the intertidal biota of the Azores and other Atlantic islands. Hydrobiologia 440:3–17.
13	Pannacciulli, F. G., J. D. D. Bishop, and S. J. Hawkins. 1997. Genetic structure of populations of two species of *Chthamalus* (Crustacea: Cirripedia) in the north-east Atlantic and Mediterranean. Marine Biology 128:73–82.
14	http://iobis.org/mapper/
15	La Gomera (MTB, 11/2013)

ID	Reference
16	Madeira (MTB, 1/2013)
17	http://www.algaebase.org/search/species/detail/?species_id=T76489787afdd60df
18	Coyer, J. A., G. Hoarau, J. F. Costa, B. Hogerdijk, E. A. Serrão, E. Billard, M. Valero, G. A. Pearson, and J. L. Olsen. 2011. Evolution and diversification within the intertidal brown macroalgae *Fucus spiralis / F. vesiculosus* species complex in the North Atlantic. Molecular Phylogenetics and Evolution 58:283–296.
19	Węsławski, J. M., M. Zajaczkowski, J. Wiktor, and M. Szymelfenig. 1997. Intertidal zone of Svalbard. Polar Biology 18:45–52.
20	http://www.algaebase.org/search/bibliography/detail/?biblio_id=c9e9a5f3e4c752b1f
21	http://www.algaebase.org/search/species/detail/?species_id=f877b167bd42f68b0&sk=0&from=results
22	http://www.algaebase.org/search/species/detail/?species_id=T29dae1de89957165&sk=0&from=results
23	Pedersen, P. M. 2011. Grønlands havalger. Epsilon. dk.
24	Hoarau, G., J. A. Coyer, M. C. W. G. Giesbers, A. Jueterbock, and J. L. Olsen. 2015. Pre-zygotic isolation in the macroalgal genus *Fucus* from four contact zones spanning 100–10 000 years: a tale of reinforcement? Royal Society Open Science 2:140538.
25	Southward, A. J. 2008. Barnacles. Field Studies Council for The Linnean Society of London and The Estaurine and Coastal Sciences Association.
26	Lüning, K. 1990. Seaweeds: their environment, biogeography, and ecophysiology. John Wiley & Sons.
27	Jones, S. J., N. Mieszkowska, and D. S. Wethey. 2009. Linking Thermal Tolerances and Biogeography: *Mytilus edulis* (L.) at its Southern Limit on the East Coast of the United States. The Biological Bulletin 217:73–85.
28	Riginos, C., and C. W. Cunningham. 2005. Invited review: local adaptation and species segregation in two mussel (*Mytilus edulis* x *Mytilus trossulus*) hybrid zones. Molecular ecology 14:381–400.
29	Hilbish, T. J., A. Mullinax, S. I. Dolven, A. Meyer, R. K. Koehn, and P. D. Rawson. 2000. Origin of the antitropical distribution pattern in marine mussels (Mytilus spp.): routes and timing of transequatorial migration. Marine Biology 136:69–77.
30	http://doris.ffessm.fr/fiche2.asp?fiche_numero=2030
31	Øvstedal, D. O., and R. I. L. Smith. 2001. Lichens of Antarctica and South Georgia: A Guide to Their Identification and Ecology. Cambridge University Press.
32	Gibson, R., B. Hextall, and A. Rogers. 2001. Photographic Guide to the Sea and Shore Life of Britain and North-west Europe. Oxford University Press, Oxford, UK.
33	Reid, D. G. 1990. Trans-Arctic migration and speciation induced by climatic change: the biogeography of *Littorina* (Mollusca: Gastropoda). Bulletin of Marine Science 47:35–49.
34	http://www.marinespecies.org/aphia.php?p=taxdetails&id=140266

ID	Reference
35	http://www.marinespecies.org/aphia.php?p=taxdetails&id=140262
36	Weslawski, J. M., J. Wiktor, M. Zajaczkowski, and S. Swerpel. 1993. Intertidal zone of Svalbard. 1. Macroorganism distribution and biomass. Polar Biology 13:73–79.
37	Węsławski, J. M., M. Zajaczkowski, J. Wiktor, and M. Szymelfenig. 1997. Intertidal zone of Svalbard. 3. Littoral of a subarctic, oceanic island: Bjornoya. Polar Biology 18:45–52.
38	Ingólfsson, A. 1996. The distribution of intertidal macrofauna on the coasts of Iceland in relation to temperature. Sarsia 81:29–44.
39	http://www.malacolog.org/search.php?nameid=47
40	Høsaeter, T. 1986. An annotated check-list of marine molluscs of the Norwegian coast and adjacent waters. Sarsia 71:73–145.
41	Graham, A. 1988. Molluscs: Prosobranchs and Pyramidellid Gastropods: Keys and Notes for the Identification of the Species. Synposes of the British Fauna (New Series). No. 2 (Second Edition). (D. M. Kermack, and R. S. K. Barnes, Eds.). Brill Archive.
42	Fretter, V., and A. Graham. 1962. British prosobranch molluscs. Their functional anatomy and ecology. Ray Society.
43	Nekhaev, I. O. 2013. Distributional notes on *Gibbula cineraria* (Linnaeus, 1758), *Pseudosetia turgida* (Jeffreys, 1870) and *Haliella stenostoma* (Jeffreys, 1858) in Russian part of the Barents Sea (Gastropoda). Ruthenica 23.
44	Smith, D. A. S. 1969. Some aspects of the biology of *Gibbula cineraria* (L.) with observations on *Gibbula umbilicalis* (Da Costa) and *Gibbula pennanti* (PHIL.).(Mollusca: Prosobranchia). Durham University.
45	Crisp, D. J., and A. J. Southward. 1958. The Distribution of Intertidal Organisms Along the Coasts of the English Channel. Journal of the Marine Biological Association of the United Kingdom 37:157–203.
46	Bazaïri, H., A. Bayed, M. Glémarec, and C. Hily. 2003. Spatial organisation of macrozoobenthic communities in response to environmental factors in a coastal lagoon of the NW African coast (Merja Zerga, Morocco). Oceanologica Acta 26:457–471.
47	Scheibling, R. E., and B. G. Hatcher. 2001. The ecology of *Strongylocentrotus droebachiensis*. Pages 271–306 *in* J. M. Lawrence, editor. Developments in Aquaculture and Fisheries Science. Elsevier.
48	http://www.algaebase.org/search/species/detail/?species_id=E73ec774871e7ea72&-session=abv4:C223DB630a5af2C318XrB06821D5
49	Vethaak, A. D., R. J. A. Cronie, and R. W. M. Van Soest. 1982. Ecology and distribution of two sympatric, closely related sponge species, *Halichondria panicea* (Pallas, 1766) and *H. bowerbanki* Burton, 1930 (Porifera, Demospongiae), with remarks on their speciation. Bijdragen tot de Dierkunde 52:82–102.
50	http://www.algaebase.org/search/species/detail/?species_id=j7fdb9763a20082eb&-session=abv4:5868C3200a6771DE57IG4F828795
51	Espinosa, F., and J. M. Guerra-García. 2005. Algae, macrofaunal assemblages and temperature: a quantitative approach to intertidal ecosystems of Iceland. Helgoland Marine Research 59:273–285.

ID	Reference
52	Munda, I.-M. 2004. The structure and distribution of Fucacean Associations in the Icelandic Coastal Area. Acta Bot. Islandica 14:103–159.
53	Guiry, M. D., J. A. West, D.-H. Kim, and M. Masuda. 1984. Reinstatement of the genus *Mastocarpus* Kützing (Rhodophyta). Taxon:53–63.
54	Monteiro, F. A., A. M. Solé-Cava, and J. P. Thorpe. 1997. Extensive genetic divergence between populations of the common intertidal sea anemone *Actinia equina* from Britain, the Mediterranean and the Cape Verde Islands. Marine Biology 129:425–433.
55	Fautin, D. G., M. Daly, and V. A. Cappola. 2005. Sea anemones (Cnidaria: Actiniaria) of the Faroe Islands: a preliminary list and biogeographic context. Pages 77–87 Annales Societatis Scientiarum Faeroensis Supplementum.
56	Chomsky, O., Y. Kamenir, M. Hyams, Z. Dubinsky, and N. E. Chadwick-Furman. 2004. Effects of temperature on growth rate and body size in the Mediterranean Sea anemone *Actinia equina*. Journal of experimental marine biology and ecology 313:63–73.
57	Gashout, S. F., and A. D. Haddoud. 2001. Libyan Lagoon Management Proceeding of Fifth International Conference on the Mediterranean Coastal Environment MEDCOAST. Pages 1033–1042 *in* D. I. Eozkan, editor. Proceeding of Fifth International Conference on the Mediterranean Coastal Environment MEDCOAST.
58	Cunningham, P. N., S. J. Hawkins, H. D. Jones, and M. T. Burrows. 1984. The geographical distribution of *Sabellaria alveolata* (L.) in England, Wales and Scotland, with investigations into the community structure of, and the effects of trampling on *Sabellaria alveolata* colonies. Report to the Nature Conservancy Council from the Department of Zoology, Manchester University, Manchester. HF3/11/22 535.
59	*Chthamalus montagui* and *C. stellatus* distributions combined
60	Firth, L. B., T. P. Crowe, P. Moore, R. C. Thompson, and S. J. Hawkins. 2009. Predicting impacts of climate-induced range expansion: an experimental framework and a test involving key grazers on temperate rocky shores. Global Change Biology 15:1413–1422.
61	Mieszkowska, N., R. Leaper, P. Moore, M. A. Kendall, M. T. Burrows, D. Lear, E. Poloczanska, K. Hiscock, P. S. Moschella, and R. C. Thompson. 2005. Marine Biodiversity and Climate Change (MarClim) Assessing and predicting the influence of climatic change using intertidal rocky shore biota. Marine Biological Association Occasional Publications.
62	Moore, J. J., and C. Howson. 2013. Surveys of the Rocky Shores in Sullom Voe.
63	Ávila, S. P., J. Azevedo, J. M. Gonçalves, J. Fontes, and F. Cardigos. 2000. Checklist of the shallow-affinity marine molluscs of the Azores: 2-São Miguel Island.
64	Kendall, M. A., M. T. Burrows, A. J. Southward, and S. J. Hawkins. 2004. Predicting the effects of marine climate change on the invertebrate prey of the birds of rocky shores. Ibis 146 Suppl 1:40–47.
65	Fransen, C., and P. Wirtz. 1997. Contribution to the knowledge of decapod crustaceans from Madeira and the Canary Islands. Zoologische Mededeelingen 71:215–230.
66	Wares, J. P. 2001. Biogeography of *Asterias*: North Atlantic climate change and speciation. The Biological Bulletin 201:95.

ID	Reference
67	Simkanin, C., A. M. Power, A. Myers, D. McGrath, A. Southward, N. Mieszkowska, R. Leaper, and R. O'Riordan. 2005. Using historical data to detect temporal change in the abundances of intertidal species on Irish shores. Journal of the Marine Biological Association of the United Kingdom 85:1329–1340.
68	O'Riordan, R. M., and N. F. Ramsay. 1999. The current distribution and abundance of the Australasian barnacle *Elminius modestus* in Portugal. Journal of the Marine Biological Association of the UK 79:937–939.
69	Harms, J., and K. Anger. 1989. Settlement of the barnacle Elminius modestus Darwin on test panels at Helgoland(North Sea): A ten year study. SCI. MAR. 53:417–421.
70	Moore, L. B. 1944. Some intertidal sessile barnacles of New Zealand. Pages 315–334 Transactions of the Royal Society of New Zealand.
71	Phillips, N. 1995. Biogeography of *Sargassum* (Phaeophyta) in the Pacific basin. Taxonomy of economic seaweeds 5:107–145.
72	Sanchez, I., C. Fernández, and J. Arrontes. 2005. Long-term changes in the structure of intertidal assemblages after invasion by *Sargassum muticum* (Phaeophyta). Journal of Phycology 41:942–949.
73	Baer, J., and D. B. Stengel. 2010. Variability in growth, development and reproduction of the non-native seaweed *Sargassum muticum* (Phaeophyceae) on the Irish west coast. Estuarine, Coastal and Shelf Science 90:185–194.
74	Brodie, J., R. H. Walker, C. Williamson, and L. M. Irvine. 2013. Epitypification and redescription of *Corallina officinalis* L., the type of the genus, and *C. elongata* Ellis et Solander (Corallinales, Rhodophyta). Cryptogamie, Algologie 34:49–56.
75	South, G. R. 1975. Common Seaweeds of Newfoundland: A Guide for the Layman. Department of Biology, Memorial University of Newfoundland.
76	Garbary, D. J., E. R. Tarakhovskaya, and others. 2013. Marine macroalgae and associated flowering plants from the Keret Archipelago, White Sea, Russia. Algae 28:267–280.
77	Smale, D. A., T. Wernberg, A. L. Yunnie, and T. Vance. 2014. The rise of *Laminaria ochroleuca* in the Western English Channel (UK) and comparisons with its competitor and assemblage dominant *Laminaria hyperborea*. Marine Ecology.
78	http://www.marinespecies.org/aphia.php?p=taxdetails&id=140626
79	Wirtz, P. 1995. One vascular plant and ten invertebrate species new to the marine flora and fauna of Madeira.
80	Carter, M. A., and J. P. Thorpe. 1981. Reproductive, genetic and ecological evidence that *Actinia equina* var. *mesembryanthemum* and var. *fragacea* are not conspecific. Journal of the Marine Biological Association of the United Kingdom 61:79–93.
81	Den Hartog, J. C., and O. Ocaña. 2003. A new endemic *Actinia* species (Actiniaria: Actiniidae) from the central Macaronesian Archipelagos. Zool Meded (Leiden) 77:229–244.
82	MarClim data 2002-2006

ID	Reference
83	Bellomio, A., K. Morante, A. Barlič, I. Gutiérrez-Aguirre, A. R. Viguera, and J. M. González-Mañas. 2009. Purification, cloning and characterization of fragaceatoxin C, a novel actinoporin from the sea anemone *Actinia fragacea*. Toxicon 54:869–880.
84	Pereira, A., C. BritoRITO, J. Sanches, C. Sousa-Santos, and J. I. Robalo. 2014. Absence of consistent genetic differentiation among several morphs of *Actinia* (Actiniaria: Actiniidae) occurring in the Portuguese coast. Zootaxa 3893:595–600.
85	Ocaña, Ó., and J. C. Den Hartog. 2002. A catalogue of actiniaria and corallimorpharia from the Canary Islands and from Madeira.
86	Boudouresque, C. F., and M. Verlaque. 2001. Ecology of *Paracentrotus lividus*. Developments in Aquaculture and Fisheries Science 32:177–216.
87	Penant, G., D. Aurelle, J.-P. Feral, and A. Chenuil. 2013. Planktonic larvae do not ensure gene flow in the edible sea urchin *Paracentrotus lividus*. Mar Ecol Prog Ser 480:155–170.
88	Mgaya, Y. D. 1995. Synopsis of biological data on the European abalone (ormer), *Haliotis tuberculata* Linnaeus, 1758 (Gastropoda: Haliotidae). Food & Agriculture Org.
89	http://www.marinespecies.org/aphia.php?p=taxdetails&id=125158
90	http://www.gbif.org/species/5259482
91	Hansen, J. R., and I. Haugen. 1989. Some observations of intertidal communities on Spitsbergen (79°N), Norwegian Arctic. Polar Research 7:23–27.
92	Engelskjøn, T. 1987. Eco-geographical relations of the Bjornoya vascular flora, Svalbard. Polar Research 5:79–127.
93	Hansen, J. R., and A. Ingólfsson. 1993. Patterns in species composition of rocky shore communities in sub-arctic fjords of eastern Iceland. Marine Biology 117:469–481.

Table S4 Spatial variation in thermal community composition metrics related to site-averaged values with local sea surface temperature and site-specific wave exposure (log_{10} summed wave fetch). All p-values <0.001 except *.

	Estimate	SE	t		Estimate	SE	t
CTDiv, Community Thermal Diversity				**CTR**			
(Intercept)	*-0.077	0.219	-0.35	(Intercept)	11.791	0.114	103.79
SST	0.205	0.020	10.51	SST	-0.170	0.010	-16.77
Wave fetch	0.327	0.038	8.71	Wave fetch	-0.130	0.019	-6.69
aCTDiv				**aCTR**			
(Intercept)	2.975	0.231	12.90	(Intercept)	11.873	0.134	88.79
SST	*0.005	0.021	0.25	SST	-0.251	0.012	-21.10
Wave fetch	0.271	0.040	6.86	Wave fetch	0.077	0.023	3.35
mCTDiv				**mCTR**			
(Intercept)	-1.286	0.186	-6.92	(Intercept)	12.119	0.225	53.79
SST	0.119	0.017	7.18	SST	-0.076	0.020	-3.76
Wave fetch	0.372	0.032	11.64	Wave fetch	-0.396	0.039	-10.22

Table S5 CTI trends in Shetland time series by site, 1984-2018

Site	SiteName	n	Estimate	SE	*p*	Long	Lat	Easting	Northing
ST1-1	West of Mioness	24	0.0207	0.0033	0.0033	-1.24	60.49	441828	1179071
ST2-3	Roe Clett	34	0.0051	0.0743	0.0743	-1.28	60.48	439437	1178127
ST3-3	Noust of Burraland	35	0.0056	0.0561	0.0561	-1.32	60.45	437201	1175186
ST3-4	Gluss Island East	31	0.0083	0.0013	0.0013	-1.31	60.47	437711	1177551
ST3-5	South of Swarta Taing	35	0.0066	0.0035	0.0035	-1.27	60.48	440160	1177901
ST4-1	Grunn Taing	35	0.0023	0.2066	0.2066	-1.31	60.49	437942	1178992
ST4-3	The Kames	35	0.0190	0.0001	0.0001	-1.30	60.47	438437	1176459
ST4-6	Voxter Ness	35	0.0046	0.0299	0.0299	-1.34	60.41	436084	1170089
ST5-1	South of Skaw Taing	35	0.0057	0.0621	0.0621	-1.28	60.48	439621	1178236
ST5-2	Jetty 3	35	0.0090	0.0111	0.0111	-1.30	60.46	438594	1175578
ST5-5	Mavis Grind (Stream 3)	35	0.0149	0.0000	0.0000	-1.38	60.39	434054	1168462
ST6-1	Fugla Ayre	34	0.0144	0.0059	0.0059	-1.32	60.44	437342	1174182
ST6-12	Scatsta Ness (cleared)	35	0.0140	0.0000	0.0000	-1.29	60.44	438874	1173544
ST6-13	Scatsta Ness (uncleared)	35	0.0104	0.0000	0.0000	-1.29	60.44	438976	1173524
ST6-2	South of Jetty 2	35	0.0324	0.0000	0.0000	-1.28	60.45	439163	1175089

Table S6 CTI trends in MarClim time series by site, 2002-2018, as linear regressions over time. n is the number of site surveys since 2002, usually annually.

IDn	Site	n	Estimate	SE	*p*	Longitude	Latitude
28	Lynmouth	14	-0.0948	0.0181	0.0002	51.2356	-3.8378
30	Menai Bridge	13	-0.0859	0.0251	0.0057	53.2207	-4.1643
33	Nefyn	12	-0.0802	0.0248	0.009	52.9430	-4.5702
56	Trevone	20	-0.0745	0.022	0.0033	50.5450	-4.9850
54	Swanage Peverill Point	14	-0.0705	0.0244	0.0135	50.6070	-1.9449
42	Porth Dafarch	12	-0.0661	0.0153	0.0015	53.2856	-4.6522
50	Sennen Cove Exposed	13	-0.0653	0.0289	0.0449	50.0780	-5.7092
35	Newquay Towan Head (Lenards Rock)	17	-0.0639	0.021	0.0082	50.4235	-5.0969
9	Cellar	14	-0.0599	0.0276	0.0506	50.3108	-4.0645
46	Portland (Pulpit Rock)	17	-0.0593	0.0277	0.0489	50.5130	-2.4600
16	Great Orme East	12	-0.0575	0.0392	0.1736	53.3321	-3.8297
31	Moelfre	11	-0.057	0.0189	0.0144	53.3490	-4.2354
25	Looe SJH site	15	-0.0548	0.0179	0.0091	50.3410	-4.4580
39	Point Lynas	11	-0.051	0.0272	0.0931	53.4111	-4.2823
15	Duckpool	17	-0.0501	0.0189	0.0184	50.8712	-4.5625
4	Brixham Shoalstone	19	-0.0494	0.0112	0.0004	50.4010	-3.4970
58	Wembury Church Reef	19	-0.0487	0.016	0.0073	50.3140	-4.0830
51	Sennen Cove Sheltered	10	-0.0487	0.0148	0.0108	50.0787	-5.7060
26	Lyme Regis Broadledge	17	-0.0456	0.0142	0.0058	50.7221	-2.9333
27	Lyme Regis MAK	14	-0.0437	0.0185	0.0357	50.7161	-2.9471
49	Rhosneigr	15	-0.0405	0.0176	0.038	53.2233	-4.5253
47	Prawle Point	18	-0.0402	0.0246	0.1215	50.2032	-3.7165
48	Prawle Point	18	-0.0402	0.0246	0.1215	50.7238	-2.9293
37	Penmaenmawr Natural	11	-0.0373	0.0272	0.2029	53.2683	-3.9440
38	Penmon North	17	-0.0346	0.0176	0.0677	53.3111	-4.0413
18	Hartland Quay	20	-0.0333	0.019	0.0966	50.9950	-4.5370
41	Porth Ceriad	11	-0.0331	0.0556	0.5667	52.7940	-4.5094
2	Aberffraw (Briach-Lwyd)	13	-0.0310	0.0209	0.1670	53.1776	-4.4899
52	South Haven	12	-0.0305	0.0151	0.0708	51.7319	-5.2845
45	Porthleven	19	-0.0305	0.0128	0.0296	50.0810	-5.3210
60	Widemouth	10	-0.0302	0.033	0.3874	50.7802	-4.5673
40	Port Gaverne	14	-0.0277	0.0245	0.2805	50.5952	-4.8259
43	Porth Neigwl	17	-0.0271	0.026	0.3143	52.7908	-4.5404
24	Looe Hannafore Pt (AJS)	13	-0.025	0.0319	0.4503	50.3465	-4.4512
53	St Ives Porthguiddan	19	-0.0238	0.0171	0.1823	50.2179	-5.4751
23	Llanbedrog	10	-0.0234	0.0344	0.5159	52.8516	-4.4742
20	Langerstone Point	14	-0.0209	0.0289	0.4834	50.2051	-3.7069
8	Cape Cornwall	17	-0.0204	0.0154	0.2061	50.1288	-5.7080
6	Bude	16	-0.0176	0.0122	0.1692	50.8362	-4.5592
61	Woolacombe	17	-0.0171	0.0135	0.2244	51.1796	-4.2161
10	Cemlyn	15	-0.0138	0.0155	0.3900	53.4134	-4.5087
12	Crackington Haven	14	-0.0135	0.0175	0.4541	50.7417	-4.6405

IDn	Site	n	Estimate	SE	*p*	Longitude	Latitude
11	Corbyn Head	12	-0.0130	0.0181	0.4865	50.4586	-3.5400
5	Broadhaven	14	-0.0130	0.0258	0.6231	51.7871	-5.1057
17	Great Orme Trwynygogarth	16	-0.0119	0.0276	0.6733	53.3327	-3.8801
22	Lizard	15	-0.0116	0.0218	0.6056	49.9590	-5.2080
3	Brighton Marina East	13	-0.0093	0.0289	0.7529	50.8221	-0.1309
32	Monkstone Point	14	-0.0069	0.0224	0.7626	51.6978	-4.6784
44	Porth Swtan	15	-0.0069	0.0136	0.6213	53.3713	-4.5595
21	Little Orme	15	-0.0015	0.0188	0.9365	53.3260	-3.7852
36	North Haven	13	0.00217	0.0202	0.9166	51.7365	-5.2819
59	West Angle Bay	14	0.00338	0.01	0.7397	51.6916	-5.1151
14	Criccieth Castle	17	0.0100	0.0196	0.6189	52.9146	-4.2412
13	Criccieth (East)	16	0.0170	0.0168	0.3300	52.9171	-4.2302
19	Holyhead	10	0.01911	0.0351	0.6012	53.3108	-4.6461
29	Martin's Haven	13	0.02524	0.0247	0.3295	51.7357	-5.2471
57	Welcombe Mouth	13	0.02871	0.0264	0.3007	50.9328	-4.5489
34	Newquay Little Fistral	11	0.03258	0.031	0.3199	50.4218	-5.1014
1	Aberdaron	14	0.0404	0.0314	0.2223	52.8003	-4.7220
7	Caernarfon (Aber Foreshore Road)	11	0.0474	0.0315	0.1675	53.1374	-4.2897
55	Trefor	11	0.05349	0.0635	0.4216	52.9992	-4.4215

Table S7 Regional average community thermal metrics at time-series sites using average abundance as weighting, expressed in °C. CTI, Community Temperature Index: abundance-weighted average of species thermal midpoints; CTDiv, variability among species' ther

SW Britain	SST	12.46			
	CTI	**CTDiv**	**CTR**	**nspp**	**Thermal bias**
All	12.13	3.90	9.20	53	-0.33
Animals	13.30	4.32	9.14	33	0.84
Macroalgae	10.12	2.01	9.54	18	-2.34
Other	12.04	0.00	6.22	2	-0.42

Shetland	SST	9.58			
	CTI	**CTDiv**	**CTR**	**nspp**	**Thermal bias**
All	9.11	1.97	9.42	31	-0.47
Animals	8.70	2.38	10.12	15	-0.88
Macroalgae	9.80	0.93	10.03	13	0.22
Other	9.80	0.12	6.05	3	0.22